38
Development and Function of Fungal Communities in Decomposing Wood

Lynne Boddy

University of Wales, College of Cardiff, Cardiff, Wales

INTRODUCTION: WOOD AS A VENUE FOR FUNGAL COMMUNITIES

Wood is a bulky, spatially determinate resource which decomposes slowly relative to most plant litter, taking on average 15–20 yr for small (< 5 cm diam) branches and over 300 yr for large trunks, in temperate forests (Boddy and Swift, 1984; Grier, 1978). These features make wood one of the best venues for studying the structure, dynamics and diversity of fungal communities since they are susceptible to direct examination, and the relatively slow rates of change facilitate detailed analysis without risk of missing vital stages.

As fungi colonize and utilize wood, or other resources, they encounter continually changing conditions, which influence decomposition and community development. Three interacting categories of factors can be distinguished which affect the fungal colonists: those which are specifically associated with the resource or substratum (resource quality), microclimate and other organisms (Fig. 1). These factors have been described in more detail elsewhere (e.g., Rayner and Boddy, 1988a, 1988b) and are only considered briefly here.

Resource Quality

Physical Structure

Access to nutrient sources is the first priority of any fungus encountering a suitable new resource. This may be considered to occur in two distinct stages: (1) entry into the wood unit, which may be hindered by physical and chemical barriers such as suberized tissues, gums and resins; followed by (2) spread within the two interconnecting systems of natural passages—one axial and one radial- provided by the cellular elements of which wood is composed. The orientation and distribution of the cellular elements, and hence of the void passages which their lumina provide, crucially affects fungal distribution.

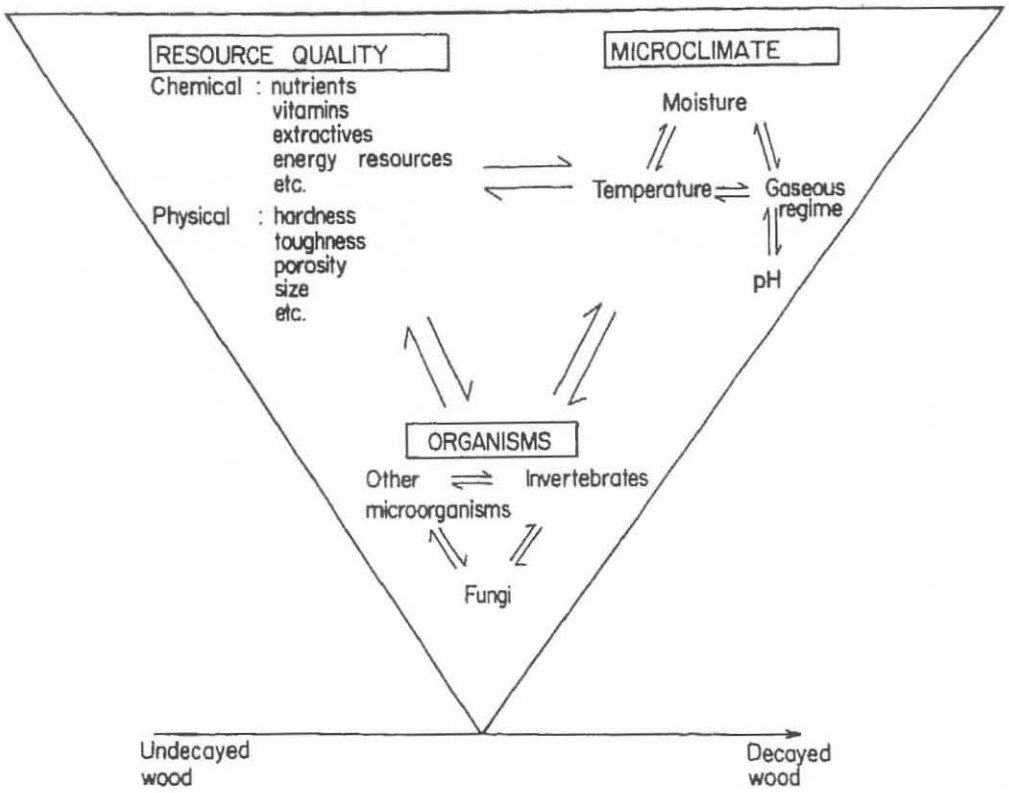


Figure 1 Scheme showing relationships between resource quality, microenvironment and decomposer organisms (From Rayner and Boddy, 1988a).

Thus, since mycelia tend to spread most rapidly along avenues of least resistance, wood-decay fungi colonize most rapidly longitudinally along the elongated lumina of xylem elements. Radial access is hindered by wood cell walls, particularly in late (autumn) wood of each annual ring where the xylem elements are closely packed; such access may also be enhanced by the nutrient-enriched parenchyma of dead medullary rays, however. Tangential spread is restricted by the general lack of any communicating system, except where a dead cambial layer facilitates subcortical spread. Hence, in the absence of interference by other factors, anatomical features give rise to longitudinally tapering, wedge-shaped columns (Fig. 2).

Availability of Organic and Mineral Nutrients

The type and availability of carbon sources is a major determinant of which fungi can colonize wood. The predominant carbon sources are the relatively refractory structural components of plant cell walls, i.e., cellulose, hemicellulose and lignin. The relative proportions of these vary between species, within species and within individual trees and change as decomposition proceeds, The dry weight composition of undecayed wood usually ranges from 40–50% cellulose, 25–40% hemicelluloses, and 18–35% lignins. Readily accessible, assimilable substrates such as starch, simple sugars, peptides and lipids constitute less than 20% of the wood dry weight, and are found almost exclusively in living or recently living parenchyma.

A wide variety of 'microfungi', i.e., Ascomycotina, Zygomycotina and Deuteromycotina with only small fruitbodies, are capable of utilizing only the relatively easily assimilable substrates. Since such substrates occur only in living or recently living wood and as breakdown products of dead hyphae, these fungi tend to be found largely at early

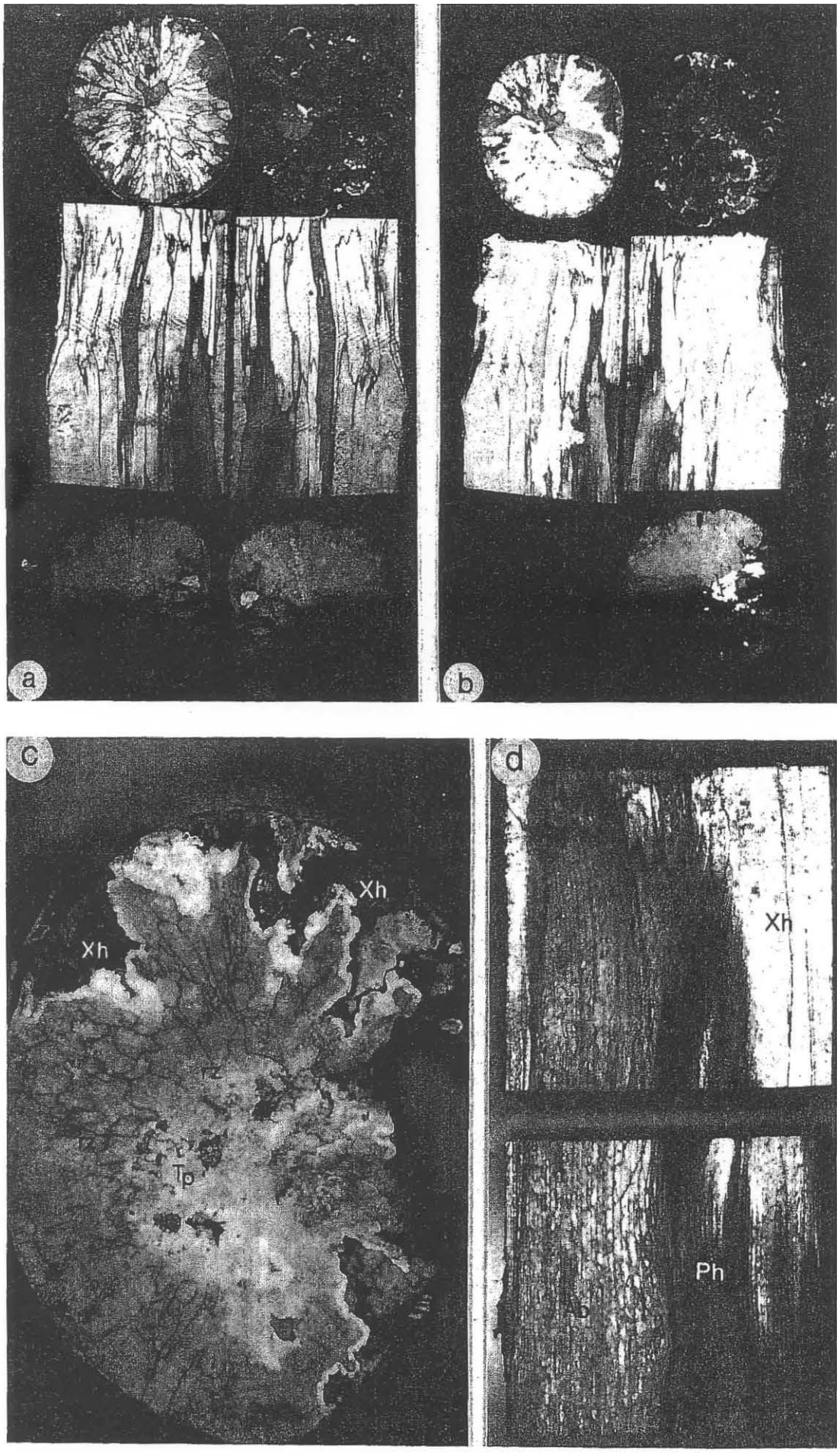
or late stages of decay or in interaction zones (see below) between wood-rotting fungi, where they probably utilize the metabolic products of the latter. Other Ascomycotina and Deuteromycotina exhibit wider enzymatic capacities and can, under suitable circumstances, cause what has been termed soft-rot, in which cellulose and hemicelluloses are degraded but lignins are not altered appreciably. This type of decay is characterized by the formation of localized erosion grooves and cavities within the wood cell wall. Because, under optimal conditions for decomposition, other types of decay are more extensive, soft-rot fungi assume prominence only under certain conditions, such as water-saturated wood, wood prone to fluctuating moisture regimes, and preservative treated wood.

The predominant fungal agents of wood decomposition are those which are capable of causing white-rot or brown-rot. White-rot is brought about by many Basidiomycotina and certain xylariaceous Ascomycotina, and involves degradation of all wood components including both cellulose and lignin. Utilization of the latter often gives the wood a bleached appearance—hence the name—and a fibrous or spongy consistency as decay proceeds. Brown-rot, which appears to be effected largely by Basidiomycotina, is characterized by loss of hemicelluloses and cellulose, with lignin left in slightly modified but essentially undegraded form. The wood is typically a light or dark brown color and at later stages becomes crumbly or powdery with a cubical pattern of cracking. The enzymatic capacities of the fungi involved in these types of decay provide them with the potential to colonize wood at all stages of decomposition.

With regard to mineral nutrient elements, attention has focused on nitrogen, probably because it is required in largest quantity by fungi. Again varying concentrations occur in different trees: the carbon-nitrogen ratio is commonly 500:1 but may range as high as 1250:1 in some species; the carbon-phosphorus ratio is greater than 3500:1 (Cowling, 1970; Swift et al., 1979). Also, within-tree differences exist, with highest concentrations in parenchyma cells, and a general decrease during the transition from sapwood to heartwood (Merrill and Cowling, 1966a, 1966c). An apparent nitrogen deficiency may be alleviated in wood-inhabiting species in several ways including preferential allocation of nitrogen and phosphorus to metabolically active cell constituents, continual autolysis and reutilization of hyphal components, and translocation of nutrients from a plentiful to a less plentiful region (Levi et al., 1968; Levi and Cowling, 1969; Wells and Boddy, 1990). Also, a high carbon to nutrient ratio may not be so unfavorable when nutrients are dispersed in insoluble substrata and are spatially concentrated (Park, 1976; Dowding, 1981).

Extractives

As well as the major nutrients mentioned above, wood contains a wide range of extraneous materials including waxes, fats, organic acids, alkaloids, oils, rosins, resins, and phenolics. Large quantities are characteristically found in heartwood, but also in other tissues particularly after wounding (Hillis, 1962). While these can act as nutrient sources or stimulants, many are fungitoxic or fungistatic to a range of wood-inhabiting fungi. Their presence, therefore, can exert a profound effect on fungal communities and may sometimes be the cause of selectivity of certain fungi for certain tree species. Examples of full or virtual specificity for certain tree genera include the heart-rot fungi *Phellinus pomaceus* on *Prunus*, *P. tremulae* on *Populus* and *Fistulina hepatica* on *Quercus* (and occasionally *Castanea*). Examples of fungi which are tolerant of the generally fungitoxic extractives of their host include *Tyromyces amarus* on incense cedar (*Calocedrus*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decurrens) (Wilcox, 1970) and *Stereum sanguinolentum* on balsam fir (*Abies balsamea*) (Etheridge, 1962). Moreover, growth of *Stereum sanguinolentum* was stimulated by volatile organic acids from *Pinus sylvestris* (Glasare, 1970) and by hexanal and α-pinene plus hexanal, although it was inhibited by monoterpenes (which are found in large quantities in living *Pinus*) (Flodin and Fries, 1978). Fungi may even grow preferentially towards some substances, e.g., *Ganoderma applanatum* towards nonanal (Fries, 1961). Not only growth but also decay rate and spore germination may be influenced by extractives (e.g., Fries, 1961; 1973a, 1973b; 1981; 1983; Hart and Shrimpton, 1979; Eslyn et al., 1981)

Microclimate

Temperature, moisture, gaseous composition and pH are the major relevant microclimatic factors affecting fungi in wood. Whilst they can be measured individually they do not vary independently (Boddy, 1984). For example, since the voids in wood act as reservoirs for both water and gases, the two are reciprocally related (Boddy, 1986). Thus, in water saturated wood O_2 concentration is low, because of its low solubility in water and the long diffusion path over which it must travel. Similarly, CO_2 concentration is relatively high. As drying proceeds water is withdrawn from progressively smaller cavities which consequently become filled by gases.

Not only do microclimatic factors affect each other, but they also work interactively on the fungi, such that the effect of, e.g., a certain water potential may be different according to, e.g., temperature. Microclimatic factors influence not only mycelial extension, germination and decay rate, but also fungal morphology, enzyme production, survival and the results of fungal interactions.

In general, wood-rotting fungi are relatively tolerant of elevated CO_2 levels, with many species able to grow at CO_2 concentrations above 70% (Hintikka and Korhonen, 1970); cord-forming Basidiomycetes appear to be less tolerant (Chapela et al., 1988; L. Boddy and O. M. Gibbon unpub.). Similarly, many fungi can grow at low O_2 concentrations, although metabolism, enzyme production and morphology may be altered considerably (Schäñel, 1976). Fungi are generally intolerant of water-saturated conditions, such as may occur in functional sapwood and ponded timber, and indeed this has been used as a means of inhibiting decay (Cartwright and Findlay, 1958; Boddy, 1986).

Figure 2 Population and community structure in beech (*Fagus sylvatica*) logs placed upright on the forest floor, as revealed by sectioning (a,d) and direct incubation (b,c). After about 2 yrs (a,b) colonization from the aerial cut surface is largely by numerous individuals of *Coriolus versicolor*, which have formed many fruit bodies, together with a few individuals of *Stereum hirsutum*. Some of the interaction zone lines appear black due to colonization by the conidial stage of *Chaetosphaeria myriocarpa*. Colonization from the base is largely by a single individual of *Phanerochaete velutina*. Replacement and deadlock phenomena are clearly visible four and a half years after felling (c,d). (c) Transverse section from near the base of the log has *Xylaria hypoxylon* (Xh) in peripheral regions although, as indicated by the presence of relic zone lines (rz), formerly it occupied almost the entire section. *Tricholomopsis platyphylla* (Tp) now occupies most of the central region, and its mycelium has grown out of the wood in various places. (d) Longitudinal section showing *X. hypoxylon* (Xh) confined to tapering columns in outer regions. In more central regions there is a gradient in color tone and texture resulting from colonizers from basal regions replacing species higher up. Replacing species include *Armillaria bulbosa* (Ab) and *Psathyrella hydrophilum* (Ph). (a and b from Coates (1984) and c and d from Chapela et al., 1988.)

Soft-rot fungi are among the most tolerant of wood-decay species, perhaps because their hyphae lie within the wood cell wall (e.g., Montgomery, 1982). With regard to growth at lower water contents, the effect of water potential varies considerably within and between taxonomic categories: Basidiomycotina tend to be intolerant, growth usually ceasing by −4.4 MPa and for cord-forming species at even higher levels; xylariaceous Ascomycotina and Deuteromycotina are much more tolerant, many being able to grow at −10 MPa and some, e.g., *Phomopsis platanoidis*, at less than −14 MPA (Boddy, 1983a; Griffith, 1989; Griffith and Boddy, 1991b). Some Basidiomycotina are, however, dominant under intermittently desiccating conditions by virtue of their survival abilities as chlamydospores etc. For example, *Schizopora paradoxa* was found to be viable after 6 years storage at less than −100MPa (Theden, 1961).

Many wood-rotting fungi are mesothermic, with cardinal temperatures in the region of 5, 25 and 40°C (Wagner and Davidson, 1954; Cartwright and Findlay 1958). However, again these values vary among species and may on occasion affect species distributions and competitive abilities. For instance, Loman (1962, 1965) found that in logging slash in Canada the four most common Basidiomycotina were remarkably consistent in their spatial location in wood, which correlated with their temperature tolerances.

Effects of pH on growth are again variable. The optima for most Basidiomycotina lie between pH 4–6, with minima between pH 2–3; brown-rot species tend to show a greater tolerance to low pH and reduced tolerance to higher pH than white-rot fungi, which correlates with the pH optima of their cellulases and hemicellulases (Henningsson, 1968; Highley, 1976). Stain fungi tolerate pH's in the range of 4–9 (Butcher 1968); many soft-rot fungi have optima in the region of pH 6 and some are still able to attain maximal extension rate at pH 8 (Duncan, 1960)

Interactions with Other Organisms

Whenever fungi are in close proximity to each other they will interact. Such interactions may be beneficial to both (mutualistic), detrimental to neither (neutralistic) or detrimental to either or both (competitive), and it is competition which considerably affects the way in which communities develop. This topic has been extensively reviewed elsewhere (Rayner and Webber, 1984; Rayner and Boddy, 1988a, 1988b) and also in this volume (see chapters by Blakeman, Culver, Lockwood, Lumsden, Wicklow); the terminology used here will follow that in the foregoing. Competition is defined as an active demand by two or more fungal individuals, of the same or different species, for the same resource. This does not necessarily imply that the resource is insufficient to satisfy the 'needs' of both, since mycelial fungi are intrinsically 'greedy' and if 'allowed' will completely occupy the entire resource. It is useful to divide competition into two types—primary resource capture and combat. The former describes the process of gaining initial access to and influence over an available resource. The latter describes events when mycelial fronts of two fungi meet. Possible outcomes include intermingling, deadlock (where neither fungus gains any of the other fungus' territory) and replacement (where one fungus ousts the other from the territory which it occupied) (Fig. 3).

While mycelial fungi usually act as the main agents of wood decomposition, other organisms may be present in rotting wood. These include bacteria, yeasts, Myxomycetes and invertebrates, particularly Insecta but also Oligochaeta, Acari and Nematoda. In some cases these organisms predominate (e.g., bacteria in waterlogged wood and termites in tropical ecosystems), but usually their major influence involves interaction with mycelial fungi which results in changes to community structure, community dynamics,

and overall decay rate. These interactions may be direct, as with grazing of fungal mycelium, antibiosis and nutrient competition, or indirect operating through alterations to the wood substratum and microclimate (Swift and Boddy, 1984).

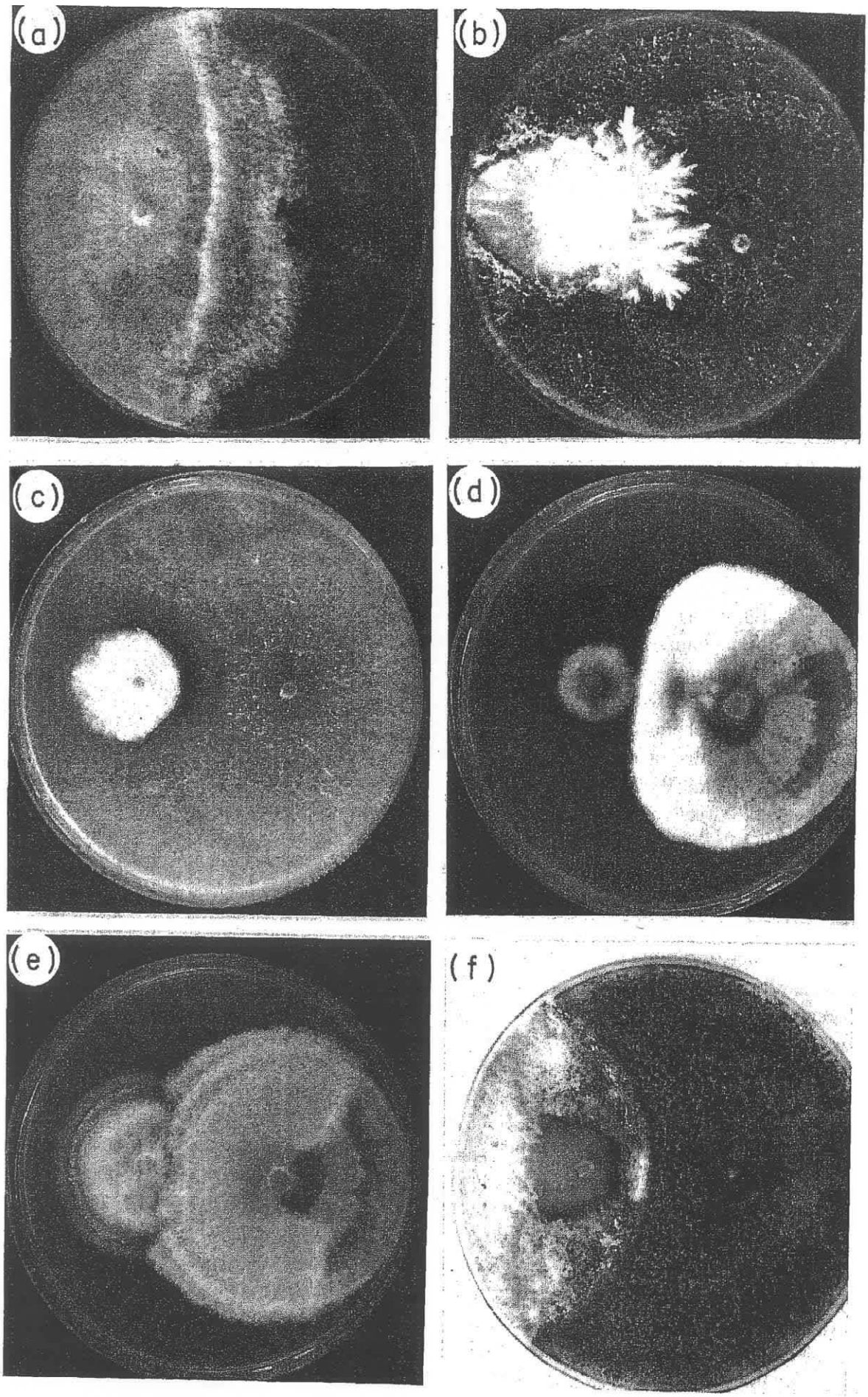
FUNGAL COMMUNITY STRUCTURE AND DEVELOPMENT IN WOOD

Community Structure and Dynamics: General Considerations

Fungal communities in wood change continually both in time and in space, a process which is often referred to as succession. This term has tended to encourage the rather simplistic view that changes occur in an ordered pattern in simple stepwise fashion. However, mycelia are three-dimensional entities, and patterns in every woody unit will differ; hence community development should be thought of as a complex, multidimensional process which follows a diverse array of 'optional' pathways (Rayner and Todd, 1979; Cooke and Rayner, 1984; Rayner and Boddy, 1988a, 1988b).

From the fungal viewpont, there are three distinct phases in the occupation and utilization of woody resources: arrival; establishment, exploitation and consolidation; and exit. Fungi may arrive at woody substrata prior to colonization as propagules or as migratory mycelium, although this difference is not always clearcut, as when dormant propagules germinate in the vicinity of a suitable resource. Accordingly, establishment processes are distinctive. Propagules may be passively dispersed to a suitable surface by a variety of mechanisms (see Ingold, 1971), lie dormant until a suitable substratum becomes available, or be inserted within wood when carried actively or passively by animals (Swift and Boddy, 1984; Malloch and Blackwell, this volume). Colonization by propagules is usually effected from localized foci where germination has occurred, since spores typically contain limited supplies of endogenous nutrients, since opportunities for input of water are limited, and since buffering against hostile environmental conditions at the resource surface is absent. Further, even if groups of propagules arrive together, among higher fungi there is little possibility of synergism if spores are genetically different, because somatic incompatibility mechanisms operate (Rayner et al., 1984). Hence the invasive force or 'inoculum potential' (sensu Garrett, 1970) which can be brought to bear by propagules is limited, and they act as an effective means of colonization only when highly favorable conditions obtain at the resource surface. Such circumstances probably occur rarely and transiently, particularly as a result of disturbance (see below). By contrast, colonization by mycelium allows synergism between hyphae, and input of nutrients and water via translocation.

After arrival, there must be a phase of resource capture during which a fungus gains access to and command over available resources. Subsequently, there follows a phase of exploitation where resources are utilized and converted into energy for growth etc. Subsequently, territorial gains must be consolidated (i.e., competitors or adverse abiotic factors resisted) or a rapid means of exit effected. Different fungi, or one fungus at different times, cope with the various situations encountered during utilization of wood to different extents and in a variety of ways. In other words, fungi fill the different types of niche available by adopting different ecological strategies (Pugh, 1980; Andrews and Rouse, 1982; Andrews, 1984a, 1984b, and this volume; Cooke and Rayner, 1984; Rayner et al., 1987b; Pugh and Boddy, 1988).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The idea underlying the concept of ecological strategies is that fungi are influenced by: (i) the incidence of competitors; (ii) stress; and (iii) disturbance. These facets of the environment lead to the development of three primary strategies—combative, stress-tolerant and ruderal, although most fungi probably display combinations of characteristics attributed to each primary strategy, and may display secondary (combination of two) or tertiary (combination of all three) strategies. These strategies can be used to define an organism's behavior at a particular time, but not to classify an organism per se, since different behavioral characteristics may be adopted under different environmental conditions, at different stages of the life-cycle or when the mycelium is in different biochemical/physiological modes (c.f., Rayner et al., 1987b; Rayner and Coates, 1987). Further, the delimitation of a type of strategy is relative and depends on what organisms are being compared. Thus, for example, wood-decay Basidiomycotina reveal ruderal, stress-tolerant and combative characteristics relative to one another, as do fungi colonizing less recalcitrant substrata, but the latter fungi may be regarded as ruderal compared to the former.

The ecological strategies adopted during different stages of utilization of organic substrata have been incorporated, by Cooke and Rayner (1984), into a scheme of community development (Fig. 4). The scheme depicts two extreme patterns of community development initiated under either high stress (i.e., extremes of microclimate and resource quality indicated above) conditions or low stress conditions following disturbance (i.e., provision of a new, uncolonized organic resource—enrichment disturbance, or destruction of resident organisms within a resource—destructive disturbance). There is a spectrum between these extremes (Cooke and Rayner, 1984), and it may be useful to incorporate a high stress/high disturbance category (Pugh, 1980; Pugh and Boddy, 1988). After initiation, subsequent community development is dictated by four determinants—stress aggravation, stress alleviation, intensification of combat and disturbance.

Under conditions of low stress/disturbance, provision of newly available resources will favor fungi with ruderal characteristics, i.e., rapid and prolific production of dispersal propagules, rapid germination, uptake of easily assimilable nutrients and primary resource capture,—an ephemeral and non-combative lifestyle. As colonization proceeds, provided that there is little further disturbance, the domains of fungi will increasingly overlap to produce a "closed" community. Persistence in the resource will increasingly depend on combative ability, either to obtain more territory and/or to defend territory already occupied. Subsequently, as decomposition nears completion, stresses tend to be imposed, particularly nutrient stress, and tolerant fungi will predominate.

Fungi which initiate community development under high stress conditions have the general characteristics of physiological adaptation, often slow germination, extension and reproduction rates, lack of combative ability, and the enzymatic capacity to utilize

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Figure 3 Interactions between *Daldinia concentrica* (right) and various wood-rotting Basidiomycotina on 2% malt agar at 25°C under different gaseous and solute potential regimes. (a) *Coriolus versicolor* replacing *D. concentrica*, atmospheric conditions. (b) *C. versicolor* growing over *D. concentrica* in the form of mycelial cords, at −1.3MPa. (c) Deadlock between *C. versicolor* and *D. concentrica* at 3.1MPa. (d) Inhibition of *D. concentrica* by *C. versicolor* under 20% O_2, 30% CO_2. (e) *D. concentrica* replacing *Peniophora lycii* under 20% O_2, 30% CO_2. (f) *D. concentrica* replacing *Peniophora quercina*. (From Boddy et al., 1985.)

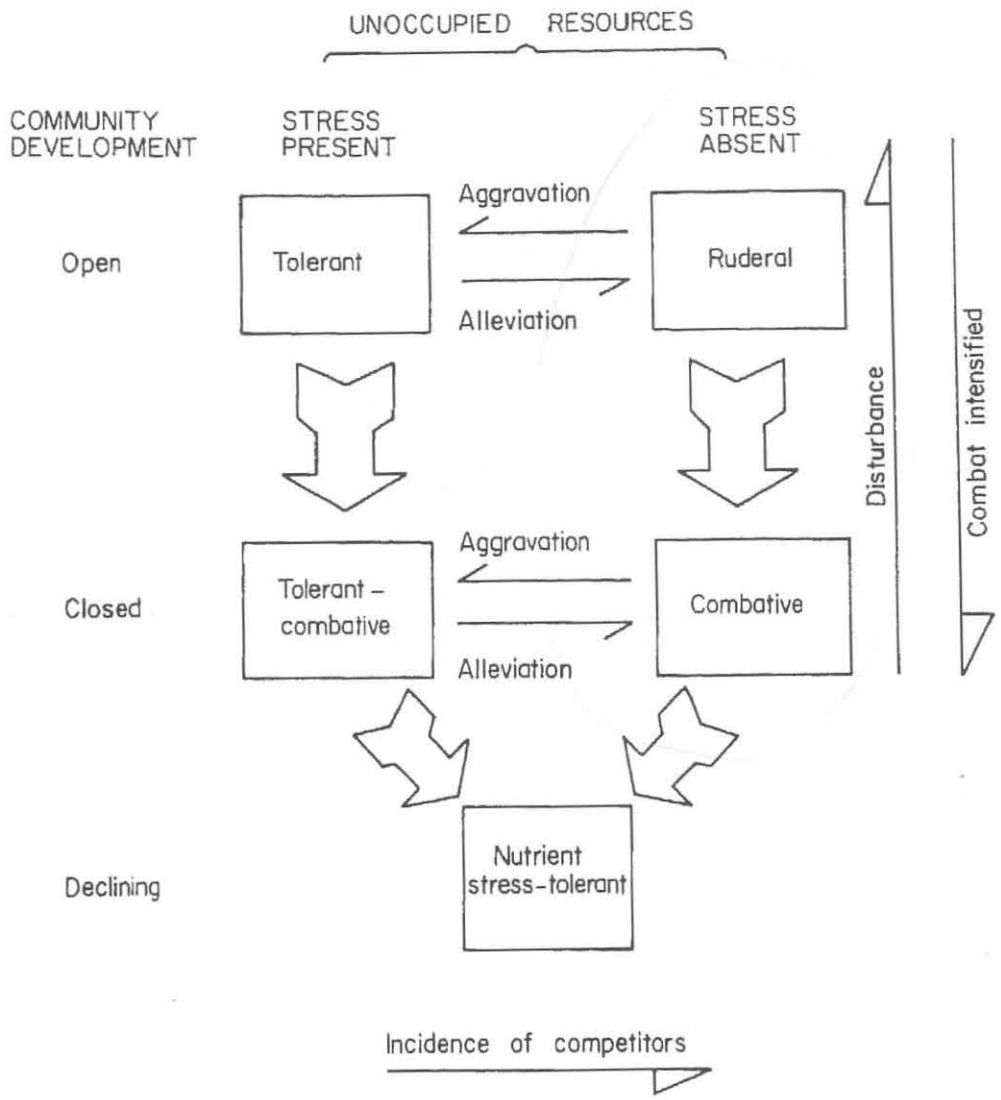


Figure 4 Diagram of community development pathways from colonization of totally unoccupied woody resources, through an open community stage with still unoccupied domain available for primary capture, to a closed community stage. The pathways culminate in a declining stage characterized by severe nutrient stress. In the absence of competitors, developing tolerant communities may progress directly to declining tolerant communities without an intermediate combative stage. (From Rayner and Webber, 1984.)

refractory substrates. High stress conditions will impose strong selection pressures, hence incidence of competitors will be limited. Nonetheless, domains will overlap when the community becomes closed and selection will be for tolerant-combative fungi. Again, at late stages nutrient stress-tolerant characteristics may be selected for.

Under high stress/disturbance conditions fungi adopting a tolerant-ruderal, secondary strategy will be at an advantage. Subsequently, tolerant-combative and then nutrient stress-tolerant strategists will ensue. Whatever the conditions when colonization is initiated, aggravation of stress will drive community development towards organisms with stress tolerant characteristics, while alleviation of stress will favor changes towards a community dominated by combative organisms. If disturbance occurs once

colonization has begun, selection will again be for organisms with ruderal characteristics. This situation frequently occurs at later stages of wood decomposition when invertebrates invade (Swift and Boddy, 1984).

Analysis of Structure and Dynamics

Methods for quantification and characterization of occurrence and activity of wood-decay fungi have been recently reviewed elsewhere (Rayner and Boddy, 1988a; Frankland et al., 1990), so the general rationale for analyzing structure will be dealt with briefly here. Much of the older information on fungi in wood was derived indirectly by removing samples, randomly or in an ordered fashion, and placing them on artificial media to allow resident microorganisms to grow out. While isolation is important there is always the possibility that isolates are contaminants. Moreover, this type of sampling approach provides a list of species, perhaps with an estimate of frequency or abundance, but little or no information on the spatial structure of the community.

The most direct means of gaining a first impression of the three dimensional structure is simply to saw wood into sections and examine the internal patterns of discolored and/or decayed regions, together with demarcating zone lines (Fig. 2). Sometimes, however, there may not be clear demarcation of separate regions; this typically occurs at early stages in the absence of white- and brown-rot fungi, and at the final stage, when extensive decomposition, particularly in association with animal activity, has all but obliterated colonization patterns. When patterns are visible, isolations can be made from each region to determine the species which occupies it. At the same time, direct incubation of the wood sections in damp chambers may allow mycelium of the fungi present in the different regions to grow out (Fig. 2b, 2c). Microscopic examination of samples of mycelium then allows identification (Stalpers, 1978; Rayner and Boddy, 1988a). That the mycelium associated with individual decay columns derives from indigenous fungi can be verified by correlating their position on separately incubated serial sections. Whether or not fungi present in spatially separate decay columns are the same genetic individual can be determined, for Basidiomycotina and xylariaceous Ascomycotina, by pairing isolates on agar plates. Intermingling indicates somatic compatibility, while production of demarcation lines indicates somatic incompatibility (Rayner et al., 1984; Rayner and Boddy, 1988a). By combining all of these approaches the 3-dimensional structure of a fungal community can be mapped (Fig. 5).

Careful observation and correlation can also provide indications of former occupation by other fungi, and hence give clues to community dynamics. Zone lines of some fungi are quite distinct, for example, those of *Oudemansiella mucida* are orange, and their presence as relics (Fig. 2c) in decay columns occupied by other fungi indicates that they were formerly present. Fruit bodies on the wood surface which do not belong to fungi present within the wood (or bark) are another indication of a former occupant. Likewise, mycelial cords and rhizomorphs extending from wood occupied by other species may also indicate prior occupancy, but care must be taken to determine whether they are arriving or departing. Presence of two species in one decay column also usually occurs only when one species is replacing another (Fig. 2d).

Further indications of which species replace which can be obtained by observing the interactions of fungi paired in model laboratory systems (Fig. 3). The simplest of these is agar culture, and interactions of wood-decay species on malt agar provide a surprisingly good 'rule of thumb' for outcomes in the field (see below). However, micro-

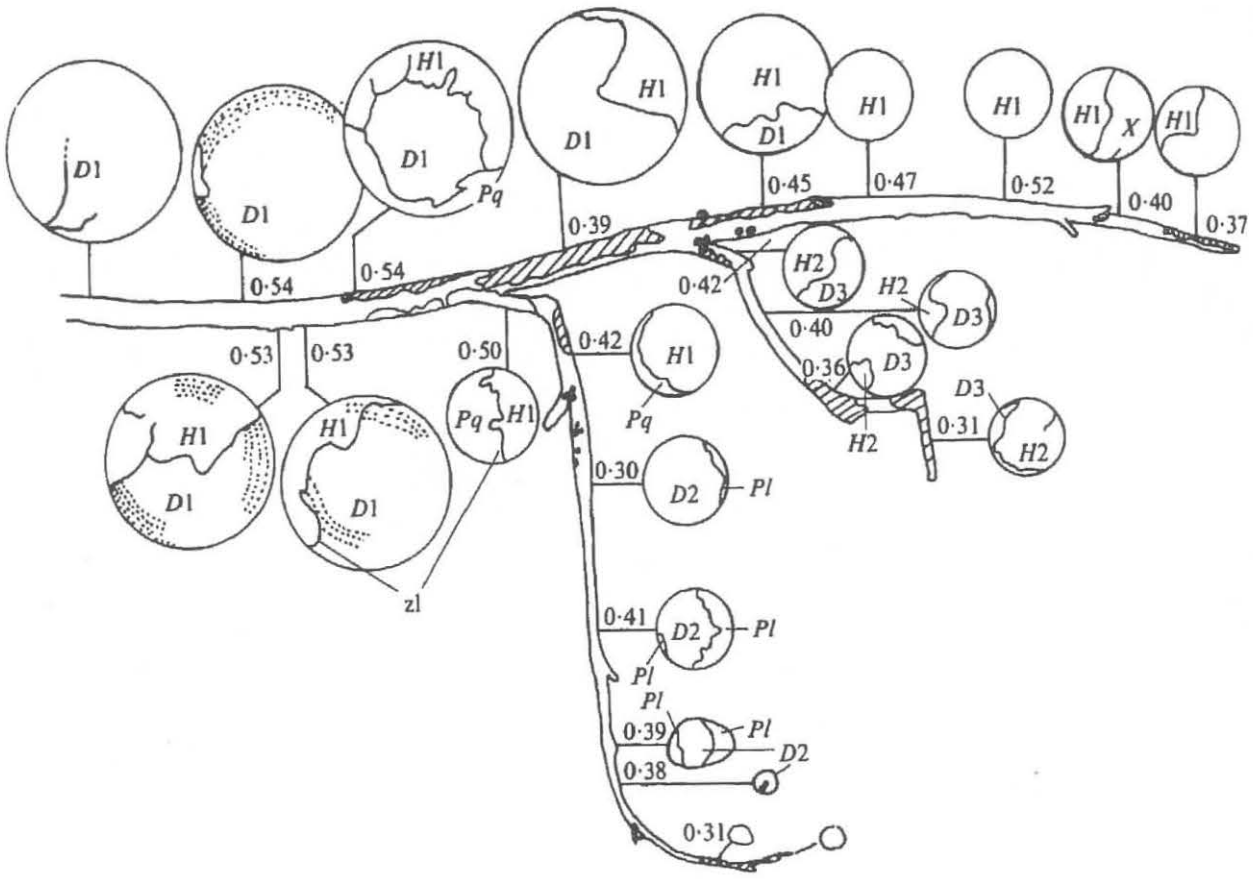


Figure 5 Decay community structure in an ash branch. Different fungal individuals were demarcated by interaction zone lines (zl) in the wood. The predominant species present were *Daldinia concentrica* (three individuals; $D_{1\text{-}3}$), *Hypoxylon rubiginosum* (H), *Peniophora lycii* (Pl) and *Peniophora quercina* (Pq). Position of fruit bodies is indicated thus: *Daldinia concentrica* ●, *Hypoxylon rubiginosum* ▨, *Peniophora lycii* □, *Peniophora quercina* □. Figures adjacent to each section represent relative density (g/cm^3). (From Boddy et al., 1985.)

climatic factors such as water potential, gaseous regime and temperature sometimes affect the outcome. Hence it is advisable to perform interactions under a variety of conditions. Interactions in wood lengths obviously better mimic the natural situation and can provide very useful information. They are, however, more time consuming, with the outcomes more difficult to discern and isolations required to determine if one species has replaced another. Since fungi that produce mycelial cords not only interact with other fungi by mycelial confrontation within wood, but also as mycelia in soil and on the surface of wood, as dedifferentiated cords which have grown through soil, it is also appropriate to perform interaction studies in model soil systems (i.e., trays of soil containing wood blocks—Fig. 6). Indeed, with some confrontations the outcomes differ according to where the interaction takes place (Dowson et al., 1989; see below). Other factors such as degree of wood decay can influence outcomes of interactions; such studies provide further information from which inferences can be drawn on the way communities develop.

Stress-Initiated Communities

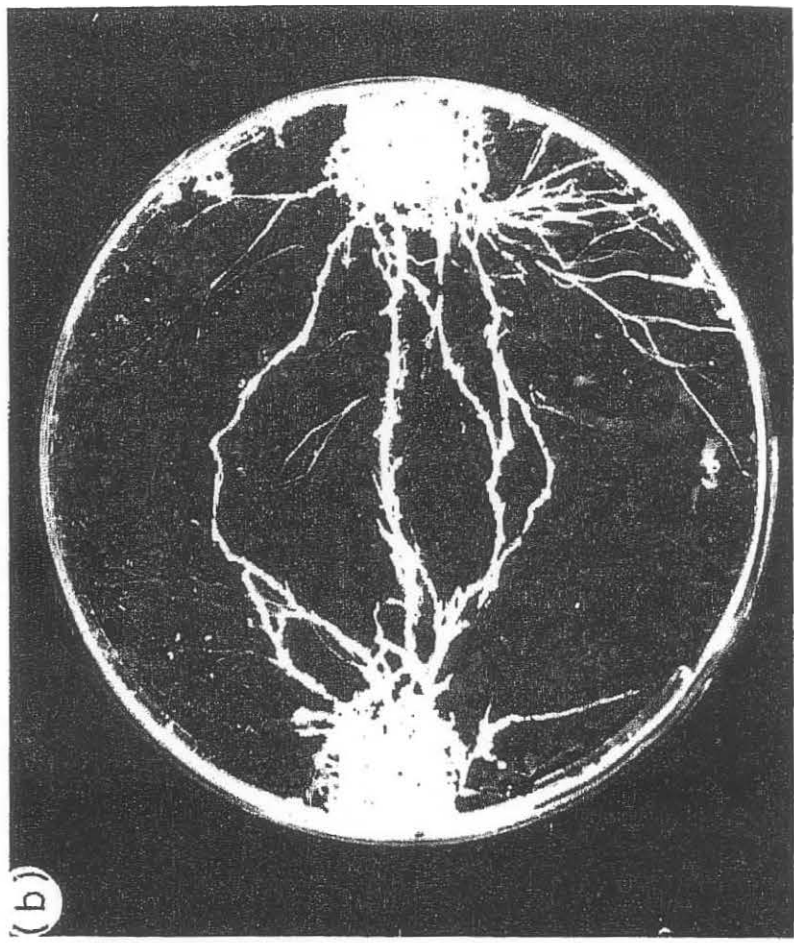
Living trees provide one of the best examples of high-stress situations in which fungal community development begins. One type of stress is provided in the heartwood of many trees which are rich in fungitoxic extractives and low in O_2. Another type occurs in sapwood which is water-saturated when functional and hence again low in O_2. Natural colonization of sapwood has been investigated most extensively in attached branches and twigs of angiosperms in the U.K., and these studies will provide the basis for the following discussion on stress-initiated community development and illustrate the means by which the process may be unravelled.

A useful initial approach is to describe the 3-dimensional community structure covering the full range of available decay states, from recently living to well decayed, using the sectioning, incubation, isolation and pairing procedures already described. This can then be followed up with artificial inoculations, addition or removal of stress, and studies on interactions, effects of microclimate and resource quality. This is illustrated below in the case studies of oak (*Quercus*) and ash (*Fraxinus excelsior*).

Case Study: Attached Oak Branches and Twigs

In oak branches, twelve white-rot Basidiomycetes characterized the decay community, and a sequence of colonization was suggested (Boddy and Rayner, 1983c). Five of these, *Peniophora quercina, Phellinus ferreus, Phlebia rufa, Stereum gausapatum* and *Vuilleminia comedens*, were attributed the role of pioneers, since they were frequently found close to functional sapwood. The latter four were found in all regions, but *Peniophora quercina* tended to be less prevalent in proximal regions. *Phlebia rufa* was found predominantly in weakened branches. They all frequently formed mycelial individuals which were several meters long and which had apparently developed in less than one growing season. Another species—the jelly fungus *Exidia glandulosa*—appeared principally to cause cambial death and loosening but did sometimes extend into sapwood. The other six species, *Coriolus versicolor, Phlebia radiata, Stereum hirsutum, Peniophora lycii, Hyphoderma setigerum* and *Schizopora paradoxa* were found in more decayed wood, had apparently replaced other species, and hence were regarded as secondary colonizers. The former three were found in all regions, *Peniophora lycii* tended to be present principally in terminal regions where branches were quite narrow (less than about 3cm diam), and *Hyphoderma setigerum* and *Schizopora paradoxa* were commonly associated with insect activity and wood prone to desiccation.

The extensive and extremely rapid development of the purported primary colonizers seemed unlikely (based on growth rates obtained on artificial media) to be effected by mycelial extension from a single focus. This led to the suggestion that they became established by a process of latent invasion whereby propagules became distributed widely but sparsely in functional sapwood in a cryptic form, but were only able to develop when the stress of high water content began to abate. If the propagules were genetically identical when their mycelia met, they would fuse to form a larger individual. To test this hypothesis, to investigate fungal origins and to confirm their roles as primary colonizers, three types of experiment were used. These were inoculation into functional sapwood, artificial stressing (by girdling) of attached branches, and incubation of healthy branches under controlled conditions in the laboratory.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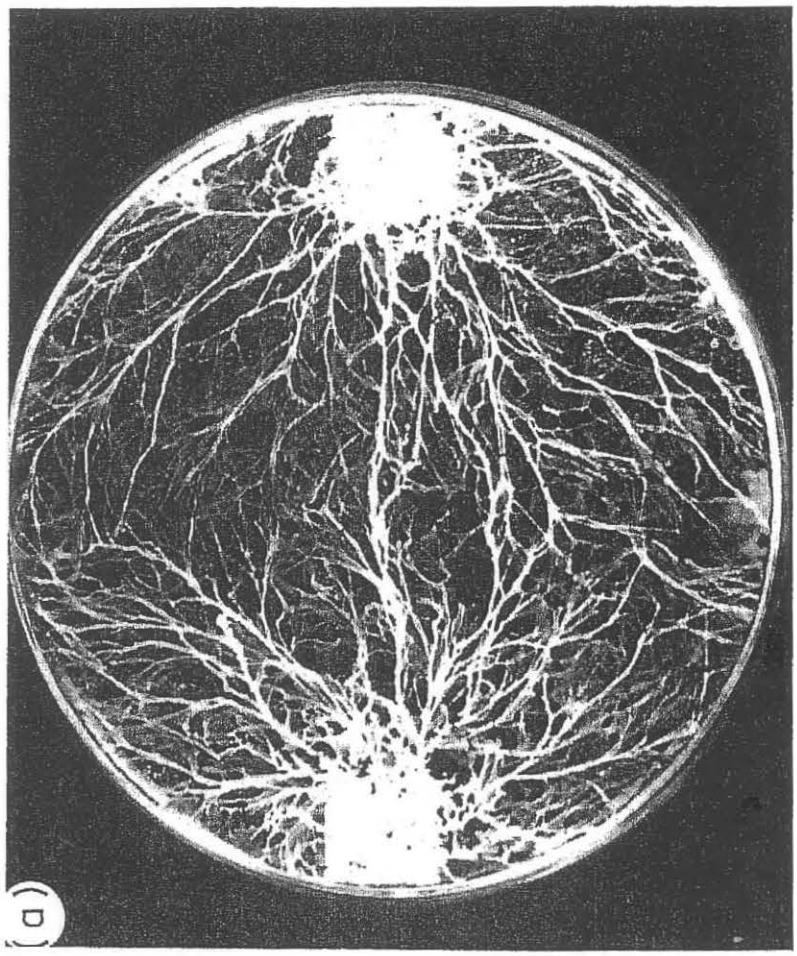
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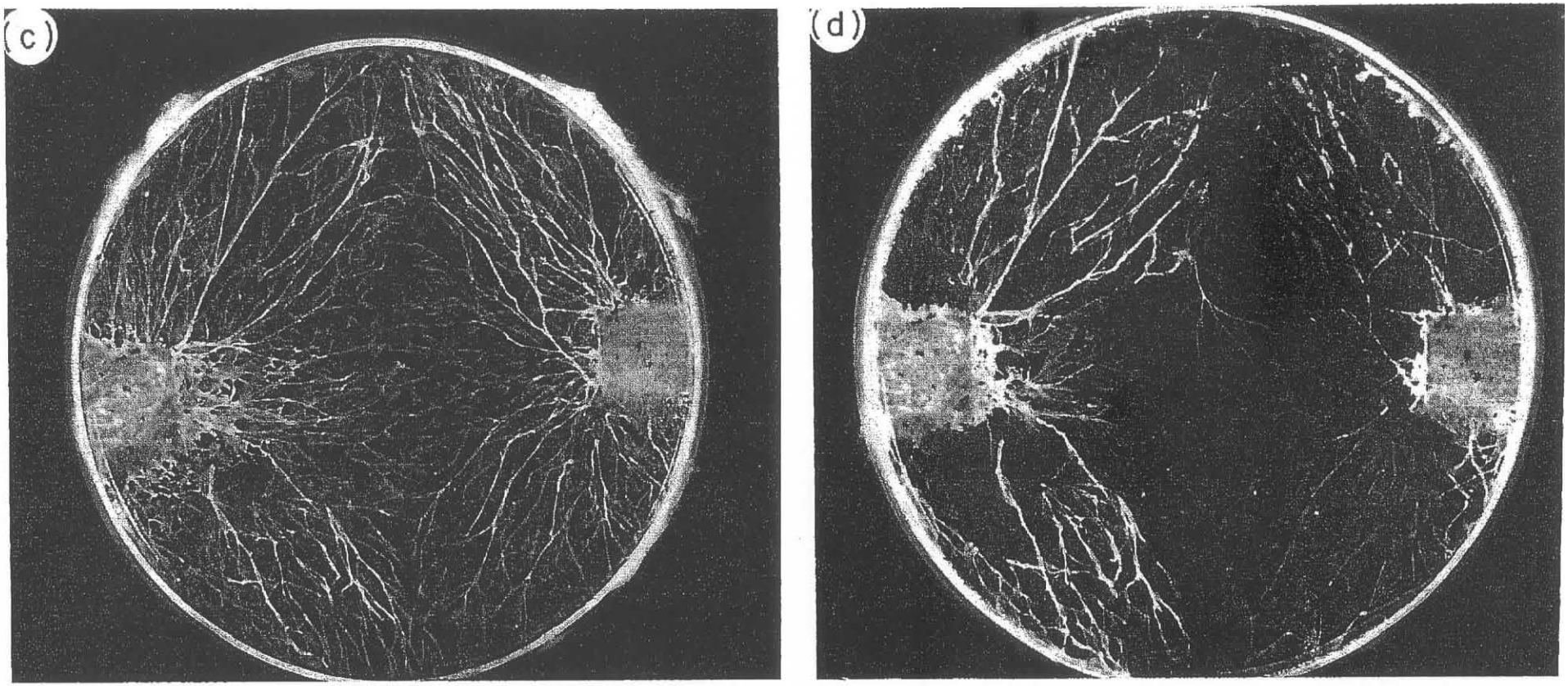

Figure 6 Interactions between mycelial cord systems of *Phanerochaete velutina* growing from beech wood blocks in 14cm diameter Petri dishes of non-sterile soil. Early (a,c) and late (b,d) stages of interaction between like genotypes (a,b), showing anastomosis followed by subsequent die-back of all but a few major cords, and antagonism between somatically incompatible mycelia (c,d). (From Rayner and Boddy, 1988a, photographs by C. G. Dowson.)

Inoculations were achieved by removing a cylinder of wood (approx. 1cm diam), inserting a similar sized plug of wood (well colonized by placing on agar cultures of the appropriate fungus) and incubating for several months (Boddy and Rayner, 1984a). Inoculated branches were sampled after 6 to 18 months, at which time they were destructively analyzed in a similar manner to naturally colonized branches. Of the fungi inoculated *Exidia glandulosa*, *Phellinus ferreus*, and *Schizopora paradoxa* failed to establish, or spread only limited distances, with the former preferentially colonizing bark. *Peniophora quercina*, *Stereum gausapatum* and *Vuilleminia comedens* readily formed localized (1.0–9.5 cm from inoculum plug) decay columns within 6 months, but apparently failed to extend further subsequently (Fig. 7a). They were, however, able to form longer decay columns (up to about 36cm after 52 wks) when branches had been stressed by removing a complete ring of bark and cambium and had begun to dry (Fig. 7b). Interestingly, in several instances individuals of these fungi, which were somatically incompati-

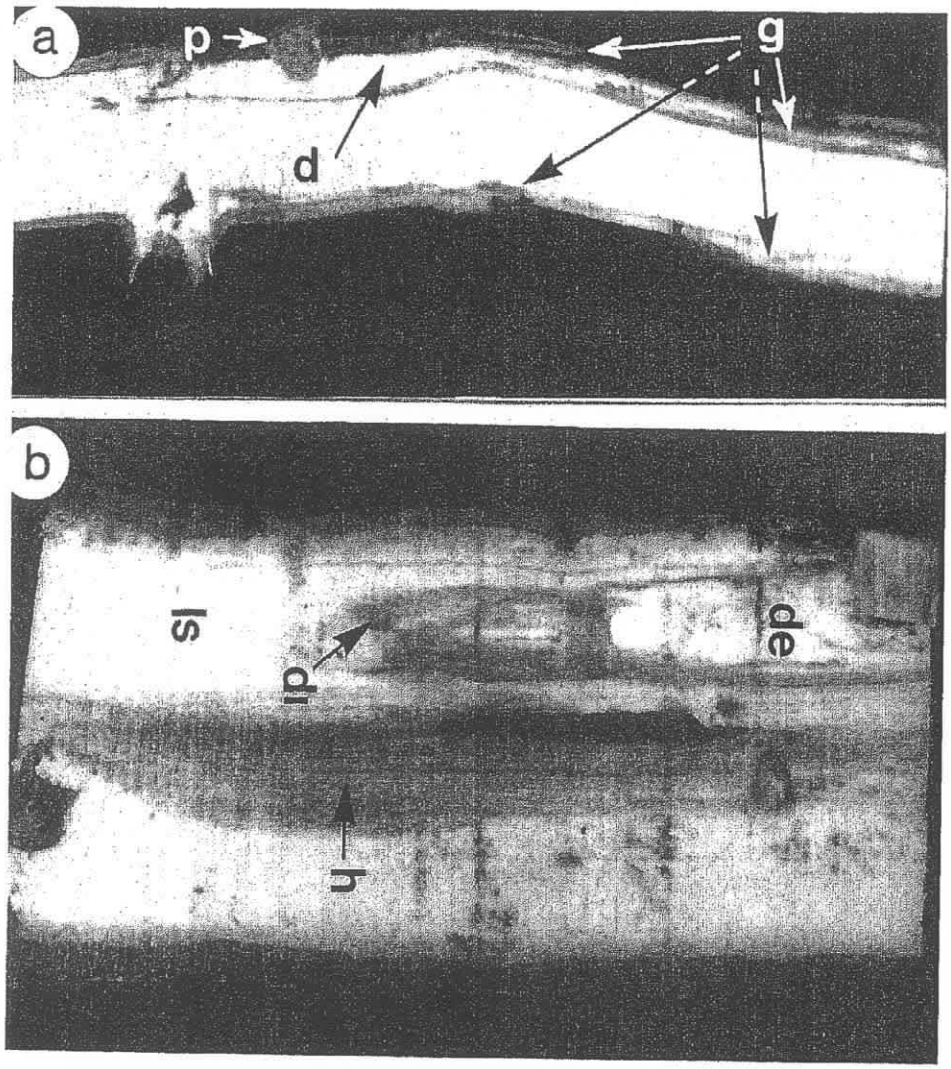

Figure 7 Longitudinal sections through attached oak branches 37 weeks after inoculation with Basidiomycotina. (a) A decay column (d) has developed from an inoculum plug (p) of *Vuilleminia comedens*. Spread towards a point of girdling (g) has been facilitated in the outermost wood. (From Boddy and Rayner, 1983.) (b) A decay column (d) developing from a plug of *Peniophora quercina* has been restricted to 6cm from the inoculum. (From Boddy and Rayner, 1984.)

ble with those inoculated, established naturally and gave rise to columns of considerable longitudinal and radial extent. This implies that the inoculated and natural colonizers established by different means, and the experiment provides some evidence that natural colonization does not occur by mycelial extension from a single focus and also that removal of high water content stress allows more extensive colonization.

Incubating healthy branches in the laboratory under controlled conditions and following the development of colonizing fungi has not been done for oak, but a detailed study has been performed on beech (*Fagus sylvatica*) (Chapela and Boddy, 1988b). Healthy branches were cut transversely into 10 cm lengths and incubated under different drying regimes, some with bark intact and others with bark completely removed, under cycling temperature of 12h at 25°C and 12h at 15°C. Branch sections were destructively sampled and isolated from over a 92d period.

Maintaining water saturation prevented the development of any fungi, but active mycelium was isolated as soon as 14d after the start of the drying period. The fungi which developed within these sections, including the Ascomycotina *Hypoxylon fragiforme, Biscogniauxia nummularium, Nectria coccinea*, the Basidiomycotina *Coniophora puteana*, and some Coelomycetes, were all proposed as primary colonizing, latent invaders in the field (Chapela, 1987; Chapela and Boddy, 1988a, 1988b). Many of these species developed inwards from the bark (and hence were absent from sections from which the bark had been removed), but *Hypoxylon fragiforme* and *Biscogniauxia nummularium* also grew out from pockets within the wood; the pockets were often abundant in certain annual rings but absent from others. Unlike the purported latent invaders from oak, genetically different individuals grew out from each pocket, as revealed by colony morphology and vegetative incompatibility tests. This was not surprising since this pattern is also seen in naturally colonized branches in the field, and simply implies that occasionally conditions are right for establishment of propagules from different sources.

To refute suggestions that these fungi colonized from external sources during the experiment, autoclaved lengths were incubated under the same conditions, and spore inoculation of *Hypoxylon fragiforme* and *Biscogniauxia nummularium* was attempted on non-autoclaved lengths. Only laboratory contaminants were found colonizing the autoclaved sections from cut ends, and neither *Hypoxylon fragiforme* nor *Biscogniauxia nummularium* colonized successfully from spores. Similar experiments with *Fagus grandifolia, Populus tremuloides* and *Corylus avellana* have also yielded primary colonizers from within functional sapwood (Chapela, 1990; L. Boddy and J. E. Hirst, unpub.; A. D. M. Rayner, unpub.). These experiments confirmed the hypotheses, proposed from the observations on oak, that early colonizers derive from inoculum latent in healthy, living/functional branches and that water content is the major determinant of their initial development.

Quite how the latent propagules become contained within the sapwood is unclear. The first suggestion was that they derived from twigs and, partly to test this, floristic studies were performed (Boddy and Rayner, 1984b; Griffith and Boddy, 1990). Although there were considerable differences between woodland sites, oak twigs did exhibit characteristic communities, the most frequently isolated species being the Basidiomycotina *Peniophora quercina* and *Vuilleminia comedens* (both of which are primary colonizers of branches), the Deuteromycotina *Cryptosporiopsis quercina* and *Cytospora ambiens*, and an unidentified sterile mycelial species. Of these the latter was also isolated from healthy bark. An incubation experiment under different drying regimes, simi-

lar to that described for beech branches, demonstrated that many of the primary colonizers of twig-wood derived from the bark (Griffith and Boddy, 1990). None of the primary colonizers of branches developed either from the bark or directly from the sapwood of oak twigs, but one species, *Cytospora ambiens*, was latently present in the wood as well as the bark.

The differences between early fungal communities in attached twigs and branches probably result from the fact that in twigs endophytes from bark can grow out and, together with fungi latently present within the wood, can colonize the whole twig, whereas in branches bark endophytes will be restricted to the immediate vicinity of the bark and not colonize the whole cross-sectional area. How the latent propagules enter oak branch sapwood is still unresolved, although via twigs remains a possibility. In beech it may be that, since those fungi which are latently present in sapwood are also bark endophytes, the fungi occasionally find their way from bark into or just beyond the cambial cells and are 'left behind' as the tree grows outwards.

When the high water content stress which obtains in functional sapwood is alleviated and mycelia grow out, the domains of individuals will encroach upon each other to form a closed community. Further, 'improved' microenvironmental conditions will allow colonization by other species arriving from external sources, but since latent invaders have positional advantage the resource will be already occupied. For primary colonizers to obtain more territory or to hold what they have, and for secondary colonizers to obtain any territory combat must ensue. To strengthen ideas (generated from observations of sectioned branches) on the way in which the community might change (Table 1), interaction studies on agar plates were performed.

The outcomes at 25°C on malt agar (Table 2) confirmed that the primary colonizers, excluding *Exidia glandulosa*, usually deadlocked against each other, although *Phlebia rufa* replaced other primary colonizers. The secondary colonizers, *Coriolus versicolor* and *Phlebia radiata* were able to replace almost all other species, although *Stereum hirsutum* was less able. *Hyphoderma setigerum* and *Schizopora paradoxa* were unable to replace any other species and were replaced by most others against which they were paired. Hence, they do not appear to maintain their presence by combative means. More probably,

Table 1 Interactions Between Basidiomycetes in Attached Oak Branches

Fungus	Replaced	Deadlock	Replaced by
Coriolus versicolor	Eg, Pq, Sg, Vc	–	–
Exidia glandulosa	–	Sg	Cv
Hyphoderma setigerum	–	–	Pra
Peniophora quercina	–	Sh, Vc	Cv
Phlebia radiata	Hs, Pru	–	–
Phlebia rufa	–	Sp	Pra
Schizopora paradoxa	Sg	Pru, Sg	–
Stereum gausapatum	–	Eg, Sp, Vc	Cv, Sp
Stereum hirsutum	–	Pq	–
Vuilleminia comedens	–	Pq, Sg	Cv

Abbreviations: Cv, *Coriolus versicolor*; Eg, *Exidia glandulosa*; Hs, *Hyphoderma setigerum*; Pl, *Peniophora lycii*; Pq, *Peniophora quercina*; Pf, *Phellinus ferreus*; Pra, *Phlebia radiata*; Pru, *Phlebia rufa*; Sp, *Schizopora paradoxa*; Sg, *Stereum gausapatum*; Sh, *Stereum hirsutum*; Vc, *Vuilleminia comedens*. (From Boddy & Rayner, 1983c).

Table 2 Interactions Between Basidiomycetes (Common in Attached Oak Branches) on 2% Malt Agar

Fungus	Replaced	Deadlock	Replaced by
Coriolus versicolor	Eg,(Hs),Pq,Pru,Sp,Sg,Sh,Vc	Pra	—
Exidia glandulosa	Sp	Sg	Cv,Hs,Pq,Pra,(Pru),Sh
Hyphoderma setigerum	Eg	Pq,Sg	(Cv),Pra,Pru,Sh
Peniophora quercina	Eg,Pf,Sp	Hs,Sp,Sg,Sh,Vc	Cv,(Pru)
Phellinus ferreus	—	Sg,Vc	Pq,Pra
Phlebia radiata	Eg,Hs,Pq,Pf,Sp,(Sh)	Cv,Pru,Sg	—
Phlebia rufa	(Eg),Hs,(Pq),(Sh),Vc	Pra	Cv
Schizopora paradoxa	—	Sg	Cv,Eg,Pq,Pra
Stereum gausapatum	—	Eg,Hs,Pq,Pf,Pra,Pru,Sp,Sh,Vc	Cv
Stereum hirsutum	Eg,Hs	Pq,Sg,Vc	Cv,(Pra),(Pru)
Vuilleminia comedens	—	Pq,Pf,Sg,Sh	Cv,Pru

Abbreviations as for Table 1.
Parenthesis indicates partial replacement only. (From Rayner & Boddy, 1983c).

they represent a deflection of the community development pathway brought about by stress aggravation -in this case desiccation as drying continues. To determine whether their mycelia were more tolerant of drier conditions than that of the other colonizers these species were grown on malt agar which had its water potential amended by addition of salts. However, none of the fungi were able to grow at low water potentials, and in fact *Hyphoderma setigerum* and *Schizopora paradoxa* were worse than most, being unable to grow at much below −3MPa (Boddy, 1983a). Growth is not the only characteristic which would give these fungi an advantage under dry conditions, however; survival would do the same, and, as already mentioned, *Schizopora paradoxa* produces resistant chlamydospores and can survive considerable periods of desiccation.

Case Study: Attached Ash Branches and Twigs

The same procedure was adopted for community analysis as for oak, but twigs were studied in more detail, and additional peripheral experiments were performed. The sequence of community development in branches was suggested as follows (Boddy et al., 1985; Boddy et al., 1987). The Ascomycotina *Daldinia concentrica* and *Hypoxylon rubiginosum* along with the Basidiomycotina *Peniophora limitata* were thought to be pioneers growing in partly living or recently dead regions. *Exidia thuretiana* was found fruiting on the bark but was not isolated from wood and appeared to cause cambial death, perhaps taking a similar role to *Exidia glandulosa* in oak. *Radulomyces confluens* and *Mycoacia uda* were secondary colonizers and were found replacing other species; however, *Daldinia concentrica* can apparently remain dominant for considerable periods, being found in trees 20 yr after felling (L. Boddy and A. D. M. Rayner, unpub.). *Peniophora limitata* and *P. violaceolivida* were also secondary colonizers but tended to occur in distal regions which were prone to desiccation. *Phomopsis platanoidis* and a sterile unidentified species (Sp. 12) were isolated occasionally. The former apparently caused little decay and was found in the proximity of the bark, although the latter was often found in decayed wood throughout the branch.

As in oak, the primary colonizers formed a few but extensive decay columns, and it was again suggested that they colonized by a process of latent invasion (Fig. 5). However, while the physical structure of the communities are analogous, the species compositions differ. This begs the questions why the primary colonizers in the two tree species were different and why *Coriolus versicolor* and *Phlebia radiata* were not secondary colonizers, despite the fact that they are common on angiospermous wood in general? Undoubtedly, multiple factors are involved, but some must relate to the resource quality and microclimatic conditions obtaining (see earlier discussion). An obvious factor is water content; ash dries much more rapidly than oak and laboratory experiments on agar media indicate that Ascomycotina grow at much lower water potentials (often less than −10 MPa) than Basidiomycotina (see above; Griffith, 1989; Griffith and Boddy, 1991b). However, there must be other reasons why *Daldinia concentrica* and *Hypoxylon rubiginosum* rather than other Ascomycotina are the primary colonizers in ash. Water does not appear to be the reason why *Coriolus versicolor* and *Phlebia radiata* are not secondary colonizers in ash, since they are more tolerant than *Radulomyces confluens*, on agar media, of reduced water potentials; also, they are able to replace other ash colonists on malt agar (Boddy et al., 1987).

While agar pairings threw no light on the differences between ash and oak communities, they did help to explain some of the changes in the fungal community structure of ash. On malt agar *Daldinia concentrica* replaced all species against which it was

paired except *Peniophora limitata* and sometimes *Peniophora lycii*. This fitted with the observation that it is dominant for considerable periods of time, but did not tie in with the fact that it is often seen deadlocking with *Hypoxylon rubiginosum* at early stages of decay. Clearly, the conditions provided by malt agar do not reflect those experienced at early stages of decay, hence pairings were subsequently incubated under a gaseous regime of 5% O_2, 30% CO_2. Pairings were also made on agar adjusted to a water potential of -2.2 MPa to simulate conditions at later stages of decay when drying occurs. Under elevated CO_2 and reduced O_2 conditions *Hypoxylon rubiginosum* did, in fact, deadlock with *Daldinia concentrica*. Interestingly, *Coriolus versicolor* could not replace *Daldinia concentrica* under a range of decreased O_2, increased CO_2 regimes, although it was the better combatant on malt agar and at reduced water potentials (Boddy et al., 1985). The purported secondary colonizer, *Radulomyces confluens*, while able to replace most species on malt agar and under the altered gaseous regime, was only occasionally able partially to replace one isolate at the lowered water potential. These differences clearly imply that a delicate balance exists within the community, which may shift when abiotic conditions change. Thus, stress alleviation and aggravation causes a shift in community development pathways not only because some fungi are better adapted to grow under different conditions than others, but also because changes in the stress regime affect mycelial interactions.

Community structure (Fig. 8) in ash twigs was assessed using the now familiar mapping, isolation and incubation techniques, and the origins of early colonizers determined by incubating twig lengths, with and without bark, under different drying regimes (Griffith and Boddy, 1988). Further, field evidence of successional sequences and

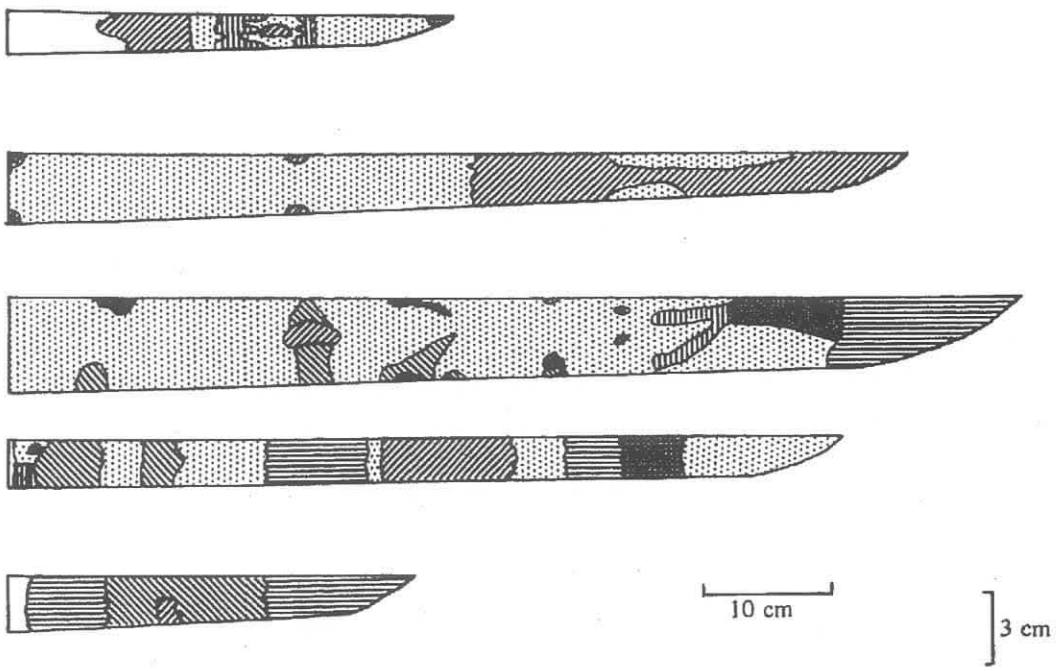

Figure 8 Maps of community structure of dead attached twigs, with bark removed, showing five representative types. Maps show whole area of the twig's surface. ▩, *Phomopsis platanoidis*; ▦, *Libertella fraxinea*; ▨, Sp. 12; ▤, *Peniophora lycii*; ▥, *Fusarium lateritium*; ■, *Acremonium* sp.; □, no fungi; ▧, incidental species. (From Griffith and Boddy, 1988.)

timescales over which changes occurred were obtained by artificially stressing attached healthy twigs by removing a complete ring of bark, cambium and recent sapwood from around the twig circumference, removing leaves and destructively sampling at intervals over a two year period (Griffith and Boddy, 1990). *Phomopsis platanoidis*, *Fusarium lateritium* and unidentified, sterile Sp. 12 were considered to be primary colonizers since they were frequently isolated from recently living twigs, were present as endophytes in bark, colonized healthy twigs from bark when incubated in the laboratory, and were the first colonizers, being present after 1–4 months, in the field experiment. An *Acremonium* sp., *Libertella fraxinea* and the Basidiomycotina *Peniophora lycii* were the major secondary colonizers, the former two being present in small pockets after about 2 months, and *P. lycii* after between 11 months and two years, and typically being found as bands in distal regions. Ash twigs were colonized by a different group of species from oak, and dominants were largely different from those in branches.

Incubation of healthy twig lengths not only revealed the presence of the primary colonizers, but also *Daldinia concentrica* grew into sapwood of twigs with bark present (Griffith and Boddy, 1990). In fact, intriguingly, *Daldinia concentrica* also developed in incubated beech and oak twig lengths, yet it was not isolated from any of the attached decaying twigs from these three tree species. While it is the predominant primary colonizer of attached dead ash branches, it is found only infrequently in dead beech and hardly ever if at all in oak (Whalley and Watling, 1980, 1984). This phenomenon may result from drying regime; twig lengths dried much more rapidly in the laboratory than in the field (Griffith and Boddy, 1990, 1991a), and it may be that *Daldinia concentrica* would develop in the field if appropriate conditions obtained. These might occur, for example, if healthy twigs are broken during a storm and remain suspended in the canopy.

Replacement of one fungus by another was usually presumed due to combative interactions. To assess this not only were interactions set up in agar culture in the laboratory, but also in twig lengths under controlled moisture regimes in the laboratory and in twig lengths resuspended in the field (Griffith and Boddy, 1991c). These studies confirmed the hypothesized sequence of events, but again water potential affected the outcome of interactions on agar. Three cm twig lengths were inoculated with single individuals of the most common fungi by placing them on agar cultures in the laboratory. These were then suspended in the canopy of an ash tree in June and sampled later. After 6 months the purported secondary colonizer, *Peniophora lycii*, was the only species which occupied twig lengths exclusively. The primary colonizers *Libertella fraxinea*, *Phomopsis platanoidis* and Sp. 12, and the secondary colonizer *Fusarium lateritium* still usually occupied large volumes but other secondary colonizers including *Epicoccum nigrum*, *Fusarium lateritium*, *Mucor hiemalis* and *Phoma macrostoma*, had begun to colonize. Occasionally *Fusarium lateritium* had been entirely replaced by *Peniophora lycii*, and an *Acremonium* sp. was almost always entirely replaced by *Peniophora lycii*, or occasionally by *Fusarium lateritium* or *Phoma macrostoma*. After 1 yr the situation was often similar although there was a tendency for further invasion by secondary colonizers.

The interactions in wood lengths were particularly instructive. In the laboratory, 3 cm lengths of ash twigs were colonized by placing them on cultures of the test fungi, then pairing in various combinations, and against uncolonized twigs, by pushing the ends together in a tight-fitting piece of rubber tubing 1cm long. These were then incubated under various water potential regimes and sampled at various time intervals (Griffith, 1989; Griffith and Boddy, 1991c). There were again differences in outcomes

under different regimes, but outcomes were largely in accord with field observations (Table 3). Unexpectedly, when *Peniophora lycii* was paired against other species it replaced them but frequently died in the lengths which it originally occupied (Fig. 9), and behaved similarly when growing into uncolonized twigs. A similar phenomenon was often observed with *Libertella fraxinea*. This explains the bands of these species which were frequently seen in attached twigs (Fig. 8).

Non-stress/Disturbance-initiated Communities

Case Study: Felled Beech Logs

Probably the best studied system is felled beech logs (Ueyama, 1966; Siepmann, 1973; Rayner 1977a, 1977b; Coates and Rayner, 1985a, 1985b, 1985c; Chapela et al., 1988; Chapela and Boddy, 1988c). The techniques of sectioning, mapping, isolation from decay columns, and pairing in agar culture were again particularly suitable for revealing community structure once closed communities had developed, although systematic sampling was more apposite at early stages before distinct decay columns developed.

The general patterns of community structure and development (Fig. 10) were similar in the different studies, although there were distinct differences in the species which colonized from the cut ends when logs were placed vertically with one end buried in the soil. This was not, however, the case when logs were placed horizontally on the ground. The first colonists of cut surfaces were mostly non-Basidiomycotina and had many R-selected characteristics. Mycelial penetration from horizontal, aerially exposed cut surfaces was slower than from that exposed to soil: an average depth of only 2–4mm was achieved from the former in the first 6 weeks after exposure, but there was no obvious lag from the latter. Aerial surface colonists were presumably subjected to more stressful conditions (particularly desiccation) than those from the soil, hence the shift in development pathways.

Colonization also occurred from within the logs, e.g., by *Hypoxylon fragiforme, Biscogniauxia nummularium, Cryptosporiopsis fasciculata, Libertella faginea, Nectria coccinea*, as a result of mycelial development of fungi which were latently present in the sapwood of the standing tree (c.f., above). Presumably because of the selective nature of the living tree, the floristic composition at early stages of decay were remarkably similar on nine different sites, despite differences in soil, litter, vegetation and season of felling (Chapela and Boddy, 1988c). Likewise there were similar increases in overall abun-

Table 3 Interactions Between Fungi Inoculated Into Ash (*Fraxinus Excelsior*) Twigs Under Field Conditions

Species	Replaced by	Partially replaced by
Phomopsis platanoidis	Au	Fl, 12, in
Acremonium sp. A	Pl, in	Au, Fl, Co, Pm
Sp. 12	Pl	Pp and Fl
Libertella fraxinea		En, Cf, in, Pm, 12
Fusarium lateritium	Pl, Tr, in	Pp, Ac
Peniophora lycii	*in*	

Au, *Aureobasidium* c.f. *pullulans*; Ac, *Acremonium* sp.; Fl, *F. lateritium*; En, *Epicoccum nigrum*; Pp, *Phomopsis platanoidis*; Cf, *Coniothyrium fuckelli*; in, incidental species; Pm, *Phoma macrostoma*; 12, Sp. 12; Tr, *Trichoderma* sp. (From Griffith, 1989)

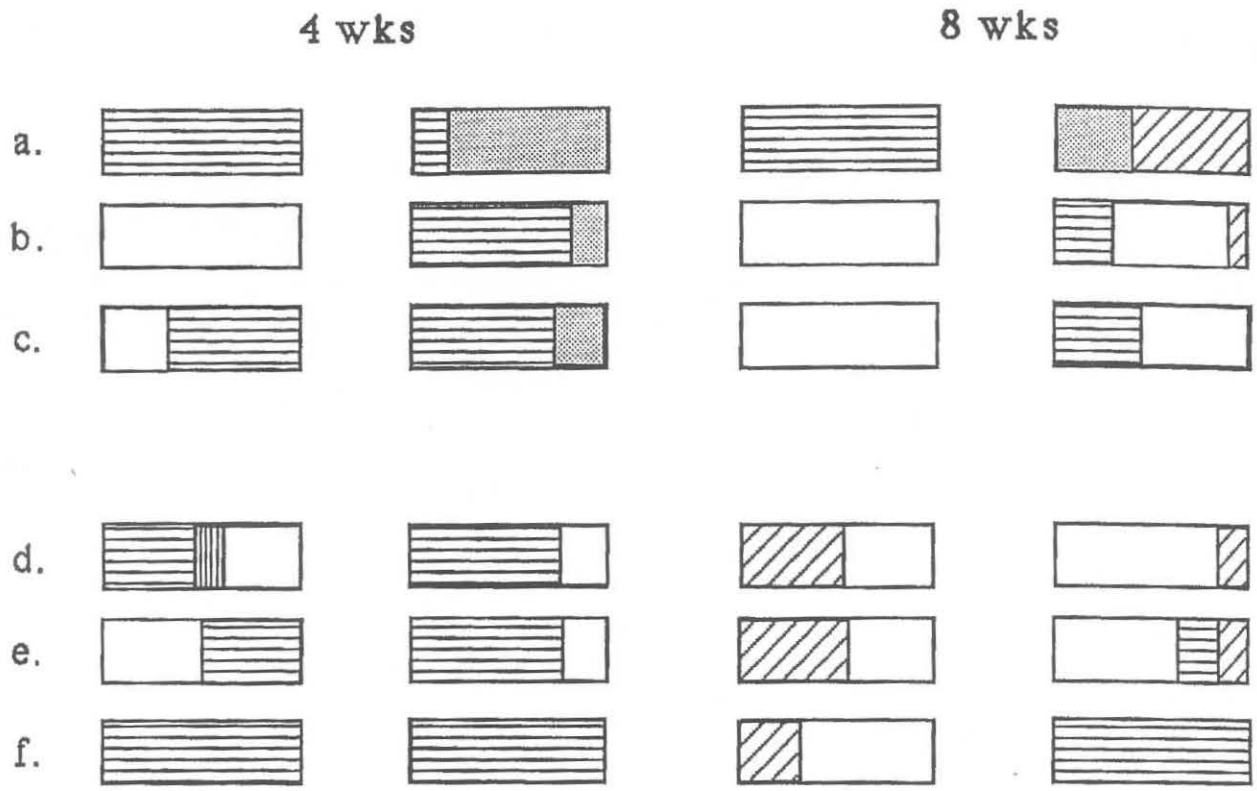

Figure 9 Diagrammatic summary of the outcomes of pairings between fungi in joined ash (*Fraxinus excelsior*) twig lengths (represented by the boxes) in the field (a and d) and under controlled moisture and temperature regimes in the laboratory (b and e, −0.8MPa at 20°C; c and f, −4.1MPa at 20°C). Originally adjacent lengths were joined together and contained *Peniophora lycii* in the twig on the left and *Phomopsis platanoidis* (a,b,c) or uncolonized (d,e,f) in the twig on the right. Shading represents the average (3 replicates) volume of wood occupied by different species after 4 and 8 weeks: ▤, *Peniophora lycii*; ▦, *Phomopsis platanoidis*; ▨, other fungi; ▥, bacteria; □, uncolonized wood. (Redrawn from Griffith, 1989.)

dance at successive samplings on most sites. The overall pattern of colonization followed a steadily increasing but decelerating course, as might be expected on resources of limited size, with continuous recruitment of new species for at least 70 weeks (Fig. 11). This constant recruitment could be interpreted as a result of 'closer packing' of species in the limited volume of wood available for colonization, but more probably is a result of new species arriving while others are declining.

Various non-Basidiomycotina, such as *Ascocoryne sarcoides*, and the Basidiomycotina *Chondrostereum purpureum* were common at early stages in discolored but not visibly decayed wood (Coates and Rayner, 1985a, 1985b, 1985c; Chapela and Boddy, 1988c). Various airborne Basidiomycotina, principally *Bjerkandera adusta*, *Coriolus versicolor* and *Stereum hirsutum*, began to establish from the aerial cut surface within a couple of weeks. Their decay columns became clearly resolved from 24 weeks onwards, but they were generally truncated at a depth of about 2 cm. Interaction zone lines between different individuals were commonly colonized by *Chaetosphaeria myriocarpa* (see above). The white-rot Ascomycotina, *Xylaria hypoxylon*, became increasingly evident from 12 to 52 weeks and extended from both aerial and buried cut surfaces at one site though only infrequently at others, perhaps relating to diameter of logs used in different experi-

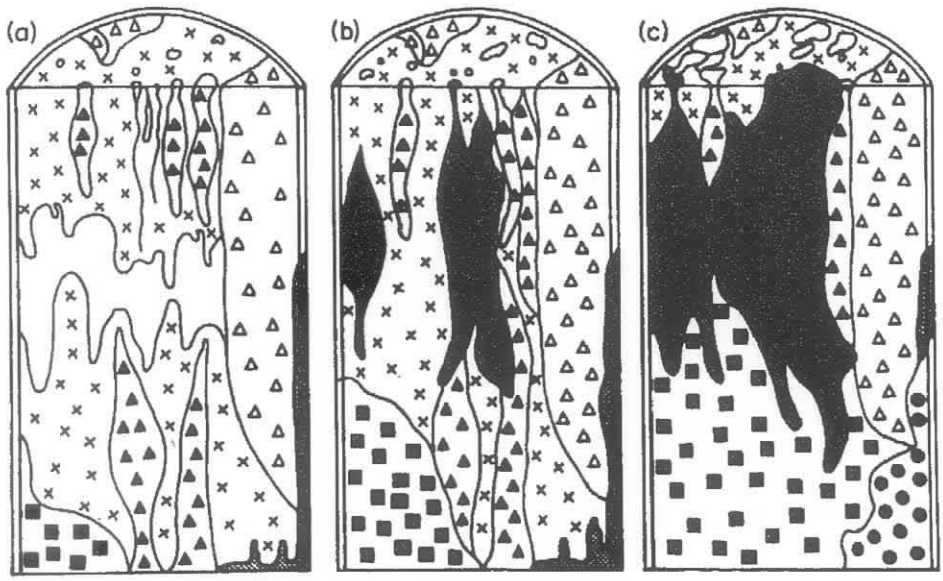

Figure 10 Idealized diagrams illustrating a typical pattern of natural decay community development in a cut beech (*Fagus sylvatica*) log placed upright on the forest floor, showing the community patterns at 6, 12 and 18 months, respectively. X, stained or discolored wood containing microfungi and/or the Basidiomycotina *Chondrostereum purpureum* and *Corticium evolvens*; ▲, *Xylaria hypoxylon*; △, *Hypoxylon nummularium*; horizontal hatching, combative airborne Basidiomycotina, e.g., *Coriolus versicolor, Bjerkandera adusta* and *Stereum hirsutum*; ■, combative early-arriving cord-formers, e.g., *Phallus impudicus* and *Tricholomopsis platyphylla*; ●, combative late-arriving cord-formers, e.g., *Phanerochaete velutina*; stipple, *Armillaria bulbosa*. (From Coates, 1984.)

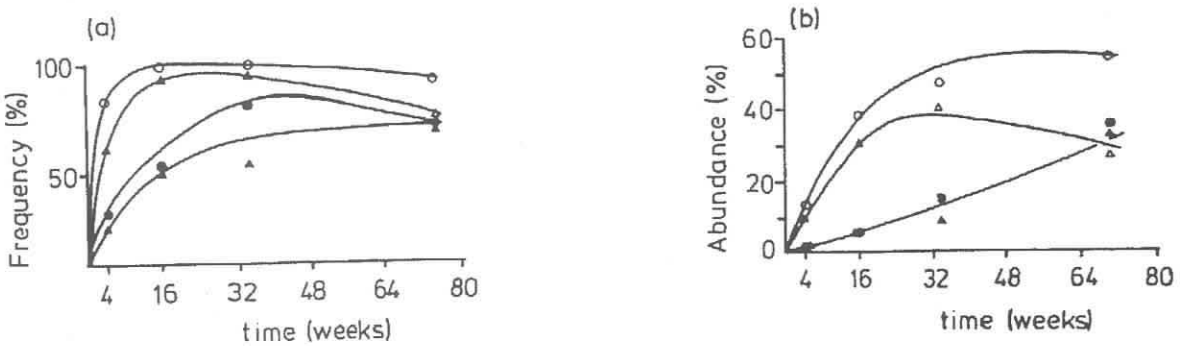

Figure 11 Frequency and abundance of isolation of different groups of fungi from beech (*Fagus sylvatica*) logs lying horizontally on the forest floor at two sites in the U.K. Open symbols, latently established colonizers; closed symbols, basidiomycetes (not latent in healthy branches). ●, site 1; ▲, site 2. (From Chapela and Boddy, 1988.)

ments. A major difference in community structure between felled logs and attached branches was that the former consisted initially of numerous small decay columns (Fig. 2, 10) reflecting colonization by prolific numbers of spores.

The rhizomorphic *Armillaria bulbosa* was present on some sites and colonized from soil, but typically caused little decay and was almost completely restricted to peripheral regions. Cord-forming species, such as *Phallus impudicus, Tricholomopsis platyphylla* and

Phanerochaete velutina, arrived at regions in ground contact within 2–3 months, depending on the proximity of logs to established systems of these fungi, but they initially grew into the wood only slowly (which is borne out by the strikingly different curves of frequency and abundance of this group, Fig. 11). They subsequently proceeded to extend upwards and eventually to occupy very large volumes of wood.

Chondrostereum purpureum was infrequent after 1 yr and *Biscogniauxia nummularium* and *Hypoxylon fragiforme* were declining after 1–1.5 yr. Likewise *Bjerkandera adusta* declined after 1.5 yr, but *Stereum hirsutum* persisted, albeit in a small number of logs, for 4.5 yr. *Coriolus versicolor* and *Xylaria hypoxylon* still occupied quite large volumes in 45 and 90 %, respectively, of logs after 4.5 yr. Cord-forming species still dominated many logs at this time, but other species, including the Basidiomycotina *Coprinus* spp., *Lenzites betulina*, *Psathyrella hydrophilum*, *Sistotrema brinkmanii*, the Ascomycotina *Lopadostoma turgidum* and various Mucorales and Deuteromycotina from soil, which had not been detected at earlier samplings, were then prevalent (Chapela et al., 1988).

The decline of some of the earlier colonizers is undoubtedly due to competitive exclusion by more combative fungi, however, this may not be so for the latent invaders of beech since a similar pattern of increase then decrease in response to gradual drying of previously water-saturated, healthy branches occurred in the laboratory in the absence of secondary colonizers (Chapela and Boddy, 1988b). Further evidence is provided by the fact that *Hypoxylon fragiforme* was only replaced by one species against which it was paired in agar culture, although *Biscogniauxia nummularium* was replaced by all but one (Chapela and Boddy, 1988c).

Many of the subsequent changes did result from combative replacements, and an hierarchy in combative ability can be seen (Coates and Rayner, 1985c; Chapela et al., 1988). In agar culture *Armillaria bulbosa*, *Xylaria hypoxylon* and *Lopadostoma turgidum* were least combative, although the former two are slightly more resistant to replacement in wood when they are surrounded by intact pseudosclerotial plates. *Coriolus versicolor* and *Stereum hirsutum* were better combatants than the first three; *Phallus impudicus*, *Phanerochaete velutina* and *Tricholomopsis platyphylla* were more combative still; and *Hypholoma fasciculare*, *Lenzites betulina*, *Psathyrella hydrophilum* and *Sistotrema brinkmanii* were most combative. This hierarchy is like a sports league in that a generally poor combatant may replace, on some or all occasions, a particular species that is overall a better combatant. Also, as mentioned earlier, environmental conditions, such as microclimate, state of decay, and whether the confrontation occurs on agar, in wood or in soil, can affect the outcome. For example, under conditions of reduced aeration cord-forming fungi, *Sistotrema brinkmanii* and *Lopadostoma turgidum* were unable to replace *Coriolus versicolor* but they could under normal atmospheric conditions, which may partly explain why *Coriolus versicolor* survived in inner volumes of wood for considerable periods of time. This may also explain why cord-forming fungi, although they often arrived rapidly at the surface of logs, were initially slow to enter wood.

Lenzites betulina adopted a particularly interesting colonization strategy. It is mycoparasitic on mycelium of *Coriolus versicolor* and does not just use mycelium of the latter as a source of nutrition, but as a means by which it can capture large volumes of wood which it can subsequently decompose (Rayner et al., 1987a). Once established it is quite combative and can defend and gain territory by the usual gross mycelial confrontations.

Two of the last colonizers, *Psathyrella hydrophilum* and *Sistotrema brinkmanii*, were not demonstrably more combative than cord-forming fungi under atmospheric

conditions, but were better under reduced aeration. Thus, again replacement may to some extent be influenced by microclimate and other factors associated with well decayed wood. This was almost certainly the case with the Ascomycotina *Lopadostoma turgidum*, which was found in well decayed areas of brown-rotted wood, but was unable to replace any other species in culture. This is probably an example of a stress-tolerant fungus which becomes dominant at a late stage of community development. The arrival of mucorales and Deuteromycotina is indicative of a 'backward' shift in the community development pathway resulting from disturbance caused by animal invasion. The comminutive activities of invertebrates are unfavorable to the majority of wood decay fungi but select for R-characteristics, and invariably alter the community structure at late stages (Swift and Boddy, 1984).

As with attached branches, inoculation of fungi can be instructive. Addition of different spore concentrations of *Bjerkandera adusta*, *Coriolus versicolor*, and *Stereum hirsutum* to aerially exposed, horizontal, cut surfaces resulted in differences in decomposition rate and fruitbody production (Coates and Rayner, 1985a, 1985c). High spore loads were associated with slow rates of decay and production of few sporocarps. This presumably results from the small size of the spatial domains which individuals are able to occupy, perhaps often too small to be able to divert nutrients to fruitbody production.

Case Study: Colonization of Standing Trees Following Wounding-misinterpretation of Observations?

Numerous studies have examined colonization of wood in standing trees wounded mechanically following forestry operations or artificially using, for example, a chisel or screwdriver (Shigo, 1967, 1972, 1979; Shortle et al., 1971; Tattar et al., 1971; Shortle and Cowling, 1976, 1978a, 1978b). Based on these it has been suggested that discoloration precedes decay and that non-Basidiomycotina and bacteria are pioneers, since they are consistently isolated from discolored regions which surround decay columns. Wood-decay Basidiomycotina have been considered to be secondary colonizers since they are only isolated from regions proximal to wounds, which are visibly undergoing decay. Further, it has been suggested that discoloration preconditions wood and is actually necessary before decay fungi can develop; the preconditioning mechanism which has been most commonly suggested involves detoxification of phenolic substances produced by the tree as a response to injury. A more complex suggestion has been that decay fungi induce discoloration, the latter then inhibiting growth of these fungi (Shortle and Cowling, 1978b).

These observations can, however, be interpreted differently. The majority of wood-decay Basidiomycotina have powerful enzyme complexes and can probably cope as well as any fungi with the compounds found in stained regions. The interpretation that Basidiomycotina necessarily colonize late is open to question because there is little information on the time they arrive as opposed to when they become dominant, and also they become established successfully following artificial inoculation (see above). Parallel patterns of community development are seen whenever a large supply of previously unoccupied resource is made available, i.e., enrichment disturbance, as described above. Thus, it is not surprising that the organisms which appear to predominate first are ubiquitous fungi with R-selected characteristics. The more combative and/or stress-tolerant fungi are probably found later simply because they arrive later and/or become established more slowly.

RELATIONSHIP BETWEEN COMMUNITY STRUCTURE AND OVERALL DECOMPOSITION

Investigators of decomposition ecology have tended to adopt one of two types of approach: either the 'black box' approach which is almost entirely process oriented, or analysis of patterns of community structure and development. Rarely are the two approaches combined, which is particularly unfortunate, since understanding the one depends on knowledge of the other. Wood is ideal for combining these approaches, and although few joint studies have as yet been performed the following examples should serve as an 'appetizer' and demonstrate their worth.

That community structure will affect overall decomposition is obvious since different fungi produce different types of rot and effect decay at different rates. For example, in felled beech logs after 4.5 yr *Xylaria hypoxylon* had brought about an average weight loss of 30%, which contrasts with 58% and 73% respectively by *Stereum hirsutum* and *Coriolus versicolor*, and almost complete decomposition by some cord-forming fungi (Chapela et al., 1988). As mentioned earlier, this experiment also indicated that the number of individuals can influence decay rate, with high spore loads resulting in slower decay (Coates and Rayner, 1985a, 1985c).

Interactions between fungi could also bring about increased decay as a result of synergistic effects, such as by the production of complementary cellulases (Hulme and Shields, 1975). Increases or decreases may also occur due to changes in metabolic rates during defence or capture of territory. Weight loss is indicative of fungal decay and could be used to detect such differences, however, since interactions (particularly replacements) may take place on a shorter time scale than is required to detect differences in weight loss, more rapid measurements ('instantaneous decay rate'), such as O_2-uptake or CO_2-evolution, are required (Boddy, 1983).

Weight loss and CO_2-evolution were measured from beech logs which had been decomposing on the forest floor for 14 months (Boddy et al., 1989). To investigate small scale variation and its causes, cubes ($8\ cm^{-3}$) were cut from different positions in relation to upper and lower surfaces and ends of the logs; these contained one individual, several individuals (as indicated by zone lines), or one fungus replacing another. Neither weight loss nor CO_2 evolution were correlated with position in log or water content, but variation in instantaneous rate could be explained in terms of species composition and, for some species, whether or not replacement was occurring. Decay rate by Ascomycotina was much less than by Basidiomycotina (Fig. 12). The most interesting result, however, was that rate of CO_2 loss from wood occupied by *Xylaria hypoxylon* alone was significantly ($P < 0.05$) slower than from wood in which it was replacing *Hypoxylon fragiforme* or *Nectria* spp.; in fact, when replacement was occurring CO_2 evolution was as high as by Basidiomycotina (Fig. 12). *Xylaria hypoxylon* when growing alone maintains very low water content in the wood which it occupies, presumably because it is surrounded by pseudosclerotial plates (Chapela et al., 1988), but when it replaces other species the water content of the wood is higher. Thus the increase in CO_2 evolution during replacement might reflect higher water contents. Indeed, it was correlated with higher water content and when *Xylaria hypoxylon* was artificially inoculated into wood cubes, the pseudosclerotial plates removed and water added to levels equivalent to those during replacement, CO_2 evolution was equivalent to that during replacement (Owens, 1989).

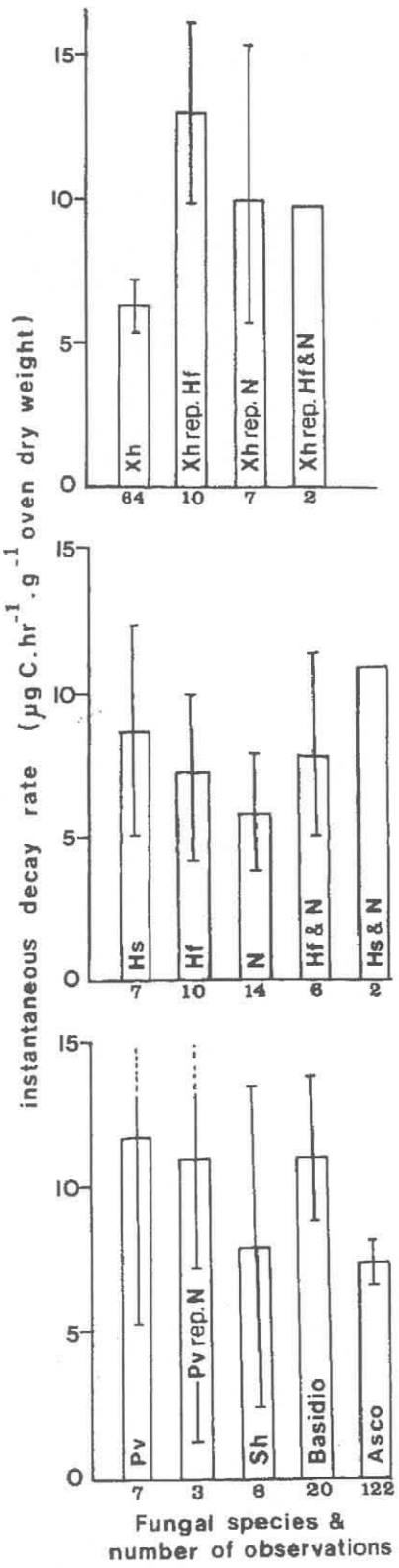

Figure 12 Instantaneous decay rate of cubes containing different fungal species cut from beech logs which had been decaying on the forest floor for 14 months. Abbreviations: Hs, *Hypoxylon serpens*; Hf, *Hypoxylon fragiforme*; N, *Nectria* sp.; Pv, *Phanerochaete velutina*; Sh, *Stereum hirsutum*; Xh, *Xylaria hypoxylon*; Asco, Ascomycotina; Basidio, Basidiomycotina; rep., replacing. (From Boddy et al., 1989.)

Interactions can be examined under controlled laboratory conditions by growing fungi individually in wood blocks and then attaching them together. CO_2 evolution can then be monitored as the interaction proceeds, and the extent of replacement can be determined by making isolations. Adopting this approach for a range of fungal pairings revealed that there were often differences between sampling times as the interaction proceeded (Owens and Boddy, in prep). Sometimes there were increases in CO_2 evolution resulting from deadlock interactions, e.g., *Stereum hirsutum* vs. *Armillaria bulbosa*, *Lenzites betulina* vs. *Flammulina velutipes*, and as one species replaced another, e.g., *Lenzites betulina* replacing *Bjerkandera adusta* and *Stereum hirsutum*. There were also instances of a decline during and following replacement, e.g., *Lenzites betulina* replacing *Coriolus versicolor*. There are probably several reasons for the increases including increased energy requirements during combat and/or rapid utilization of the opponents mycelium during replacement. Reasons for decreases are less obvious.

REFERENCES

Andrews, J. H. (1984a). Life history strategies of plant parasites. *Adv. Pl. Pathol. 2*: 105–130.

Andrews, J. H. (1984b). Relevance of r- and K-theory to the ecology of plant pathogens. In *Current Perspectives in Microbial Ecology*, M. J. Klung and C. A. Reddy (Eds.). American Society for Microbiology, Washington D.C., pp. 1–7.

Andrews, J. H., and Rouse, D. I. (1982). Plant pathogens and the theory of r- and K-selection. *Amer. Nat. 120*: 283–296.

Boddy, L. (1983a). The effect of temperature and water potential on growth rate of wood-rotting basidiomycetes. *Trans. Brit. Mycol. Soc. 80*: 141–149.

Boddy, L. (1983b). Microclimate and moisture dynamics of wood decomposing in terrestrial ecosystems. *Soil Biol. Biochem. 15*: 149–157.

Boddy, L. (1983c). Carbon dioxide release from decomposing wood: effect of water content and temperature. *Soil Biol. Biochem. 15*: 501–510.

Boddy, L. (1984). The micro-environment of basidiomycete mycelia in temperate deciduous woodlands. In *The Ecology and Physiology of the Fungal Mycelium*, D. H. Jennings and A. D. M. (Eds.). Cambridge University Press, Cambridge, pp. 261–289.

Boddy, L. (1986). Water and decomposition processes in terrestrial ecosystems. In *Water, Fungi and Plants*, P. G. Ayres and L. Boddy (Eds.). Cambridge University Press, Cambridge, pp. 375–398.

Boddy, L., Bardsley, D. W., and Gibbon, O. M. (1987). Fungal communities in attached ash branches. *New Phytol. 107*: 143–154.

Boddy, L., Gibbon, O. M., and Grundy, M. A. (1985). Ecology of *Daldinia concentrica*: effect of abiotic variables on mycelial extension and interspecific interactions. *Trans. Brit. Mycol. Soc. 85*: 201–211.

Boddy, L., Owens, E. M., and Chapela, I. H. (1989). Small scale variation in decay rate within logs one year after felling: effect of fungal community structure and moisture content. *FEMS Microbiol. Ecol. 62*: 173–194.

Boddy, L., and Rayner, A. D. M. (1983a). Origins of decay in living deciduous trees: the role of moisture content and re-appraisal of the expanded concept of tree decay. *New Phytol. 94*: 623–641.

Boddy, L., and Rayner, A. D. M. (1983b). Mycelial interactions, morphogenesis and ecology of *Phlebia radiata* and *Phlebia rufa* from oak. *Trans. Brit. Mycol. Soc. 80*: 437–448.

Boddy, L., and Rayner, A. D. M. (1983c). Ecological roles of basidiomycetes forming decay communities in attached oak branches. *New Phytol. 93*: 77–88.

Boddy, L., and Rayner, A. D. M. (1984a). Internal spread of fungi inoculated into attached oak branches. *New Phytol. 98*: 155–164.

Boddy, L., and Rayner, A. D. M. (1984b). Fungi inhabiting oak twigs before and at fall. *Trans. Brit. Mycol. Soc. 82*: 501–505.

Boddy, L., and Swift, M. J. (1984). Wood decomposition in an abandoned beech and oak coppiced woodland in south-east England. III. Decay rate and turnover time of twigs and branches. *Holarctic Ecol. 7*: 229–238.

Butcher, J. A. (1968). The ecology of fungi infecting untreated sapwood of *Pinus radiata*. *Can. J. Bot. 46*: 1577–1589.

Cartwright, K. St. G., and Findlay, W. P. K. (1958). *Decay of Timber and its Prevention* (2nd edition). H.M.S.O., London.

Chapela, I. H. (1987). *Fungal Communities in Beech Branches*. Ph.D. Thesis, University of Wales, Cardiff, Wales, U.K.

Chapela, I. H. (1990). Fungi in healthy stems and branches of American beech and trembling aspen: a comparative study. *New Phytol. 113*: 65–75.

Chapela, I. H., and Boddy, L. (1988a). Fungal colonization of attached beech branches. I. Early stages of development of fungal communities. *New Phytol. 110*: 39–45.

Chapela, I. H., and Boddy, L. (1988b). Fungal colonization of attached beech branches. II. Spatial and temporal organization of communities arising from latent invaders in bark and functional sapwood, under different moisture regimes. *New Phytol. 110*: 47–57.

Chapela, I. H., and Boddy, L. (1988). The fate of early fungal colonizers in beech branches decomposing on the forest floor. *FEMS Microbiol. Ecol. 53*: 273–284.

Chapela, I. H., Boddy, L., and Rayner, A. D. M. (1988). Structure and development of fungal communities in beech logs, four and a half years after felling. *FEMS Microbiol. Ecol. 53*: 59–70.

Coates, D. (1984). *The Biological Consequences of Somatic Incompatibility in Wood Decaying Basidiomycetes and Other Fungi*. Ph.D. Thesis, University of Bath, Bath, England.

Coates, D., and Rayner, A. D. M. (1985a). Fungal population and community development in beech logs. I. Establishment via the aerial cut surface. *New Phytol. 101*: 153–171.

Coates, D., and Rayner, A. D. M. (1985b). Fungal population and community development in beech logs. II. Establishment via the buried cut surface. *New Phytol. 101*: 173–181.

Coates, D., and Rayner, A. D. M. (1985c). Fungal population and community development in beech logs. III. Spatial dynamics, interactions and strategies. *New Phytol. 101*: 183–198.

Cooke, R. C., and Rayner, A. D. M. (1984). *Ecology of Saprotrophic Fungi*. Longman, London.

Cowling, E. B. (1970). Nitrogen in forest trees and its role in wood deterioration. *Acta Universitatius Upsaliensis 164*.

Dowding, P. (1981). Nutrient uptake and allocation during substrate exploitation by fungi. In *The Fungal Community: Its Organization and Role in the Ecosystem*, D. T. Wicklow and G. C. Carroll (Eds.). Marcel Dekker, New York, pp. 621–635.

Dowson, C. G., Rayner, A. D. M., and Boddy, L. (1989). The form and outcome of mycelial interactions involving cord-forming decomposer basidiomycetes in homogeneous and heterogenous environments. *New Phytol. 109*: 423–432.

Duncan, C. G. (1960). Soft-rot in wood and toxicity studies on causal fungi. *Proc. Am. Wood Pres. Assoc. 56*: 27–35.

Eslyn, W. E., Bultman, J. D., and Jurd, L. (1981). Wood decay inhibition by tropical hardwood extractives and related compounds. *Phytopathology 71*: 521–524.

Etheridge, D. E. (1962). Selective action of fungus-inhibiting properties of balsam fir heartwood. *Can. J. Bot. 40*: 1459–1462.

Flodin, K., and Fries, N. (1978). Studies on volatile compounds from *Pinus sylvestris* and their effect on wood-decomposing fungi. II. Effects of some volatile compounds on fungal growth. *Eur. J. For. Path. 8*: 300–310.

Frankland, J. C., Dighton, J., and Boddy, L. (1990). Methods of studying the ecology of fungi in soil and forest litter. In *Methods in Microbial Ecology*, R. Grigorova and J. R. Norris (Eds.). Academic Press, London, New York, pp. 343–404.

Fries, N. (1961). The growth-promoting activity of some aliphatic aldehydes on fungi. *Svensk Bot. Tidskr. 55*: 1–18.

Fries, N. (1973a). Effects of volatile organic compounds on the growth and development of fungi. *Trans. Brit. Mycol. Soc. 60*: 1–21.

Fries, N. (1973b). The growth-promoting activity of terpenoids on wood-decomposing fungi. *Eur. J. For. Path. 3*: 169–180.

Fries, N. (1981). Recognition reactions between basidiospores and hyphae in *Leccinum*. *Trans. Brit. Mycol. Soc. 77*: 9–14.

Fries, N. (1983). Intra- and interspecific basidiospore homing reactions in *Leccinum*. *Trans. Brit. Mycol. Soc. 81*: 559–561.

Garrett, S. D. (1970). *Pathogenic Root-Infecting Fungi*. Cambridge University Press, Cambridge.

Glasare, P. (1970). Volatile compounds from *Pinus sylvestris* stimulating the growth of wood-rotting fungi. *Arch. Mikrobiol. 72*: 323–343.

Grier, C. C. (1978). A *Tsuga heterophylla—Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Can. J. For. Res. 8*: 198–200.

Griffith, G. S. (1989). Fungal Community Structure and Development in Attached Angiosperm Twigs. Ph.D. Thesis, University of Wales, Cardiff, Wales.

Griffith, G. S., and Boddy, L. (1988). Fungal communities in attached ash (*Fraxinus excelsior*) twigs. *Trans. Brit. Mycol. Soc. 91*: 599–606.

Griffith, G. S., and Boddy, L. (1990). Fungal decomposition of attached angiosperm twigs. I. Decay community development in ash, beech and oak twigs. *New Phytol. 116*: 407–415.

Griffith, G. S., and Boddy, L. (1991a). Fungal decomposition of attached angiosperm twigs. II. Moisture relations of ash twigs. *New Phytol. 117*: 251–257.

Griffith, G. S., and Boddy, L. (1991b). Fungal decomposition of attached angiosperm twigs. III. Effect of water potential and temperature on fungal growth, survival and decay of wood. *New Phytol. 117*: 259–269.

Griffith, G. S., and Boddy, L. (1991c). Fungal decomposition of attached angiosperm twigs. IV. Effect of water potential on interactions between fungi on agar and in wood. *New Phytol. 117*: 633–641.

Hart, J. H., and Shrimpton, D. M. (1979). Role of stilbenes in resistance of wood to decay. *Phytopathology 69*: 1138–1143.

Henningsson, B. (1968). Ecology of decomposition in birch and aspen. In *Biodeterioration of Materials*, A. H. Walters and J. J. Elphick (Eds.). Elsevier, Amsterdam, London, New York, pp. 408–423.

Highley, T. L. (1976). Hemicelluloses of white- and brown-rot fungi in relation to host preference. *Mat. Org. 11*: 33–46.

Hillis, W. E. (1962) (Ed.). *Wood Extractives*. Academic Press, New York, London.

Hintikka, V., and Korhonen, K. (1970). Effects of carbon dioxide on the growth of lignicolous and soil-inhabiting Hymenomycetes. *Comm. Inst. For. Fenn. 62* (2): 1–22.

Hulme, M. A., and Shields, J. K. (1975). Antagonistic and synergistic effects for biological control of decay. In *Biological Transformation of Wood by Microorganisms*, W. Liese (Ed.). Springer-Verlag, New York, pp. 52–63.

Ingold, C. T. (1971). *Fungal Spores: Their Liberation and Dispersal*. Clarendon Press, Oxford.

Levi, M. P., Merrill, W., and Cowling, E. B. (1968). Role of nitrogen in wood deterioration. VI. Mycelial fractions and model nitrogen compounds as substrates for growth of *Polyporus versicolor* and other wood-destroying and wood-inhabiting fungi. *Phytopathology 58*: 628–634.

Levi, M. P., and Cowling, E. B. (1969). Role of nitrogen in wood deterioration. VII. Physiological adaptation of wood-destroying and other fungi to substrates deficient in nitrogen. *Phytopathology 59*: 460–468.

Loman, A. A. (1962). The influence of temperature on the location and development of decay fungi in lodgepole pine logging slash. *Can. J. Bot. 40*: 1545–1559.

Loman, A. A. (1965). The lethal effect of periodic high temperatures on certain lodgepole pine slash decaying basidiomycetes. *Can. J. Bot. 43*: 334–338.

Merrill, W., and Cowling, E. B. (1966a). The role of nitrogen in wood deterioration: amount and distribution of nitrogen in fungi. *Phytopathology 56*: 1083–1090.

Merrill, W., and Cowling, E. B. (1966b). Role of nitrogen in wood deterioration: amounts and distribution of nitrogen in tree stems. *Can. J. Bot. 44*: 1555–1580.

Merrill, W. E., and Cowling, E. B. (1966c). Role of nitrogen in wood deterioration. IV. Relationship of natural variation in nitrogen content of wood to its susceptibility to decay. *Phytophathology 56*: 1324–1325.

Montgomery, R. A. P. (1982). The role of polysaccharidase enzymes in the decay of wood by basidiomycetes. In *Decomposer Basidiomycetes: Their Biology and Ecology*, J. C. Frankland, J. N. Hedger and M. J. Swift (Eds.). Cambridge University Press, Cambridge, pp. 51–65.

Owens, E. M. (1989). *Fungal Community Structure and Functioning in Decomposing Wood*. Ph.D. Thesis, University of Wales, Cardiff, Wales.

Park, D. (1976). Carbon and nitrogen levels as factors influencing fungal decomposers. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*, J. M., Anderson and A. Macfadyen (Eds.). Blackwell Scientific Publications, Oxford, pp. 41–59.

Pugh, G. J. F. (1980). Strategies in fungal ecology. *Trans. Brit. Mycol. Soc. 75*: 1–14.

Pugh, G. J. F., and Boddy, L. (1988). A view of disturbance and life strategies in fungi. *Proc. Royal Soc. Edin. 94B*: 3–11.

Rayner, A. D. M. (1977a). Fungal colonization of hardwood stumps from natural sources. I. Non-basidiomycetes. *Trans. Brit. Mycol. Soc. 69*: 291–302.

Rayner, A. D. M. (1977b). Fungal colonization of hardwood stumps from natural sources. II. Basidiomycetes. *Trans. Brit. Mycol. Soc. 69*: 303–312.

Rayner, A. D. M., and Boddy, L. (1988a). *Fungal Decomposition of Wood: Its Biology and Ecology*. John Wiley, Chichester, New York, Brisbane, Toronto, Singapore.

Rayner, A. D. M., and Boddy, L. (1988b). Fungal Communities in the decay of wood. *Adv. Microbial Ecol. 10*: 115–166.

Rayner, A. D. M., Boddy, L., and Dowson, C. G. (1987a). Temporary parasitism of *Coriolus* spp. by *Lenzites betulina*: a strategy for domain capture in wood decay fungi. *FEMS Microbiol. Ecol. 45*: 53–58.

Rayner, A. D. M., Boddy, L., and Dowson, C. G. (1987b). Genetic interactions and developmental versatility during establishment of decomposer basidiomycetes in wood and tree litter. In *SGM Symposium 41, Ecology of Microbial Communities*, M. Fletcher, T. R. G. Gray and J. G. Jones (Eds.). Cambridge University Press, Cambridge, pp. 83–123.

Rayner, A. D. M., Brasier, C. M., and Moore, D. (Eds.) (1987). *Evolutionary Biology of Fungi*. Cambridge University Press, Cambridge.

Rayner, A. D. M., and Coates, D. (1987). Regulation of mycelial organization and responses. In *Evolutionary Biology of the Fungi*, A. D. M. Rayner, C. M. Brasier and D. Moore (Eds.). Cambridge University Press, Cambridge, pp. 115–136.

Rayner, A. D. M., Coates, D., Ainsworth, A. M., Adams, T. J. H., Williams, E. N. D., and Todd, N. K. (1984). The biological consequences of the individualistic mycelium. In *The Ecology and Physiology of the Fungal Mycelium*, D. H. Jennings and A. D. M. Rayner (Eds.). Cambridge University Press, Cambridge, pp. 509–540.

Rayner, A. D. M., and Todd, N. K. (1979). Population and community structure and dynamics of fungi in decaying wood. *Adv. Bot. Res. 7*: 333–420.

Rayner, A. D. M., and Webber, J. F. (1984). Interspecific mycelial interactions—an overview. In *The Ecology and Physiology of the Fungal Mycelium*, D. H. Jennings and A. D. M. Rayner (Eds.). Cambridge University Press, Cambridge, pp. 383–417.

Schäñel, L. (1976). Role of carbon dioxide in growth and decaying activity of wood-rotting fungi. *Folia Fac. Sci. Nat. Univ. Purkynianae Bruneusis 17*: 5–54.

Shigo, A. L. (1967). The early stages of discoloration and decay in living hardwoods in northeastern United States: a consideration of wound-initiated discoloration and heartwood. *IUFRO Congr. Proc. 9*: 117–133.

Shigo, A. L. (1972). Succession of microorganisms and patterns of discoloration and decay after wounding in red oak and white oak. *Phytopathology 62*: 256–259.

Shigo, A. L. (1979). Tree decay—an expanded concept. *U.S. Department of Agriculture Forest*

Information Bulletin, No. 419.
Shortle, W. C., and Cowling, E. B. (1976). Development of discoloration, microorganisms, and decay in living sweetgum and yellow poplar trees. *Org. Holz. 3*: 213–220.
Shortle, W. C., and Cowling, E. B. (1978a). Development of discoloration, decay and microorganisms following wounding of Sweetgum and Yellow poplar trees. *Phytopathology 68*: 609–619.
Shortle, W. C., and Cowling, E. B. (1978b). Interaction of live sapwood and fungi commonly found in discolored and decayed wood. *Phytopathology 68*: 617–623.
Shortle, W. C., Tattar, T. A., and Rich, A. E. (1971). Effects of some phenolic compounds on the growth of *Phialophora melinii* and *Fomes connatus*. *Phytopathology 61*: 552–555.
Siepmann, R. (1973). Isolierung und Bestimmung von Basidiomyceten und anderen Pilzen aus waldlagerndem Buchenholz (*Fagus sylvatica*). *Mat. Org. 8*: 271–294.
Stalpers, J. A. (1978). Identification of wood-inhabiting Aphyllophorales in pure culture. *Studies in Mycology, Baarn 16*: 1–248.
Swift, M. J., and Boddy, L. (1984). Animal-microbial interactions during wood decomposition. In *Invertebrate-Microbial Interactions*, J. M., Anderson, A. D. M. Rayner and D. W. H. Walton (Eds.). Cambridge University Press, Cambridge, pp. 89–131.
Swift, M. J., Heal, D. W., and Anderson, J. M. (1979). *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific, Oxford.
Tattar, T. A., Shortle, W. C., and Rich, A. E. (1971). Sequence of microorganisms in constituents associated with discoloration and decay of Sugar Maples infected with *Fomes connatus*. *Phytopathology 61*: 556–558.
Theden, G. (1961). Untersuchungen über die Fähigkeit holzzerstorender Pilze zur Trockenstarre. *Angew. Bot. 35*: 131–45.
Ueyama, A. (1966). Studies on the succession of higher fungi on felled beech logs (*Fagus crenata*) in Japan. *Mat. Org. 1*: 325–332.
Wagner, W. W., and Davidson, R. W. (1954). Heartrots of living trees. *Bot. Rev. 20*: 61–134.
Wells, J. M., and Boddy, L. (1990). Wood decay, and phosphorus and fungal biomass allocation, in mycelial cord systems. *New Phytol. 116*: 285–295.
Wells, J. M., Hughes, C., and Boddy, L. (1990). The fate of soil-derived phosphorus in mycelial cord systems of *Phanerochaete velutina* and *Phallus impudicus*. *New Phytol. 114*: 595–606.
Whalley, A. J. S., and Watling, R. (1980). *Daldinia concentrica* versus *Daldinia vernicosa*. *Trans. Brit. Mycol. Soc. 74*: 399–406.
Whalley, A. J. S., and Watling, R. (1984). An unusual habitat for *Daldinia concentrica*. *Bull. Brit. Mycol. Soc. 18*: 126–127.
Wilcox, W. W. (1970). Tolerance of *Polyporus amarus* to extractives from incense cedar heartwood. *Phytopathology 60*: 919–923.